

Intrasexual Competition and Body Weight Dimorphism in Anthropoid Primates

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ABSTRACT Body weight dimorphism in anthropoid primates has been thought to be a consequence of sexual selection resulting from male-male competition for access to mates. However, while monogamous anthropoids show low degrees of weight dimorphism, as predicted by the sexual selection hypothesis, polygynous anthropoids show high variation in weight dimorphism that is not associated with measures of mating system or sex ratio. This observation has led many to debate the role of other factors such as dietary constraints, predation pressure, substrate constraints, allometric effects, and phylogeny in the evolution of anthropoid weight dimorphism. Here, we re-evaluate variation in adult body weight dimorphism in anthropoids, testing the sexual selection hypothesis using categorical estimates of the degree of male-male intrasexual competition ("competition levels"). We also test the hypotheses that interspecific variation in body weight dimorphism is associated with female body weight and categorical estimates of diet, substrate use, and phylogeny. Weight dimorphism is strongly associated with competition levels, corroborating the sexual selection hypothesis. Weight dimorphism is positively correlated with increasing female body weight, but evidence suggests that the correlation reflects an interaction between overall size and behavior. Arboreal species are, on average, less dimorphic than terrestrial species, while more frugivorous species tend to be more dimorphic than folivorous or insectivorous species. Several alternative hypotheses can explain these latter results. Weight dimorphism is correlated with taxonomy, but so too are competition levels. We suggest that most taxonomic correlations of weight dimorphism represent "phylogenetic niche conservatism"; however, colobines show consistently low degrees of weight dimorphism for reasons that are not clear. *Am J Phys Anthropol* 103:37–68, 1997. © 1997 Wiley-Liss, Inc.

In most anthropoid primates, males are larger than females. Ever since Darwin (1871), body weight sexual dimorphism has been thought to be a product of sexual selection, largely through the mechanism of male-male combat for access to reproductive females. Sexual selection theory predicts that males should gain reproductive advantages over other males by fighting to exclude them from mating access to females. Thus, if

large body size assists males in winning fights, then selection should favor the evolution of large male body size. Consistent with this hypothesis, the males of most dimorphic anthropoids fight either to defend groups of

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females from other males, or for position within a male dominance hierarchy that presumably confers reproductive advantages to dominant individuals (Cowlshaw and Dunbar, 1991).

Numerous studies have examined the role of sexual selection and other factors in the evolution of body weight dimorphism in anthropoid primates. On the one hand, as predicted by the sexual selection hypothesis, monogamous anthropoids show on average less weight dimorphism than polygynous anthropoids (Fig. 1). On the other hand, several observations suggest that sexual selection is not the only factor that plays a role in the evolution of body weight dimorphism. For example, there is no correlation between body weight dimorphism and sex ratio among polygynous primates (Clutton-Brock et al., 1977; Martin et al., 1994). Among polygynous anthropoids, body weight dimorphism is highly variable, with a number of species showing little body weight dimorphism even though males compete intensely for access to mates (Leutenegger and Kelly, 1977; Martin et al., 1994). Body weight dimorphism is negligible in most prosimians, even though many are polygynous (Kappeler, 1990, 1991; Martin et al., 1994). Recently, these observations led Martin et al. (1994, p. 174) to state that "... there has, as yet, been no convincing demonstration of a link between sexual dimorphism in body weight and the level of competition among males for access to females."

Stemming partly from these observations, a variety of studies has investigated the contribution of other factors to the evolution of interspecific variation in weight dimorphism among anthropoid primates. These include phylogenetic inertia (Cheverud et al., 1985; Ely and Kurland, 1989), allometric effects (Leutenegger and Cheverud, 1982, 1985; Gaulin and Sailer, 1984; Godfrey et al., 1993; Leutenegger and Kelly, 1977; Phillips-Conroy and Jolly, 1981), energetic constraints associated with diet (Milton, 1985; Ford, 1994; Leutenegger and Kelley, 1977), sex differences in male and female energetic requirements (Clutton-Brock et al., 1977; Coelho, 1974; Demment, 1983; Pickford, 1986), selection for reduced female size in order to increase reproductive output (Mar-

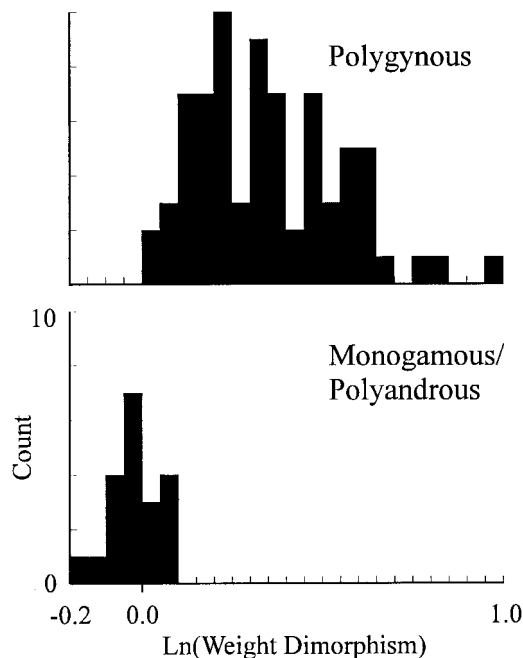


Fig. 1. Frequency histograms of ln-transformed estimates of body weight dimorphism (male/female weights) for a sample of 86 anthropoid primates, showing the distribution of dimorphism between monogamous/polyandrous species and polygynous species. Axes are the same for each histogram.

tin et al., 1994), the degree of arboreality (Clutton-Brock et al., 1977; Gautier-Hion and Gautier, 1985; Leutenegger and Kelly, 1977), predation pressure (Anderson, 1986; Clutton-Brock et al., 1977; Leutenegger and Kelly, 1977; Rowell and Chism, 1986), and variation in the ontogenetic mechanisms producing body weight dimorphism (Shea, 1986; Leigh, 1992, 1995). These various hypotheses are usually evaluated through comparative analysis of the relation between body weight dimorphism and measures of life-history variables, diet, substrate use, mating system (or sex ratio), and taxonomy. These factors are not necessarily mutually exclusive, and the relative contribution of each to the evolution of body weight dimorphism is still debated (Ford, 1994; Kappeler, 1990, 1991; Martin et al., 1994; Mitani et al., 1996).

Recent studies by Ford (1994) and Mitani et al. (1996) suggest that sexual selection via the mechanism of male-male competition for

access to mates plays an important role in the evolution of body weight dimorphism. However, the analysis of Ford (1994) is limited to platyrrhines, while that of Mitani et al. (1996) employs data on operational sex ratios for only 18 anthropoid species, a sample too small to evaluate concomitantly the relation between body weight dimorphism and other variables such as diet, substrate, or phylogeny in anthropoids. Here, we re-evaluate the relation between body weight dimorphism and estimates of male-male competition, substrate, diet, increasing body weight (allometric effects), and phylogeny in anthropoid primates. For reasons outlined below, we do not evaluate the hypothesis that dimorphism reflects reductions in female body size associated with selection for increased reproductive rate. We follow the approach of Plavcan and van Schaik (1992) and Plavcan et al. (1995) for canine dimorphism, so that the results of the separate analyses of canine dimorphism and weight dimorphism can easily be compared.

MATERIALS AND METHODS

Body weight data

We gathered from the literature data on adult male and female body weights for 86 anthropoid species (see Appendix A). Comparative analyses commonly use body weight data compiled from both primary and secondary sources (e.g., Ford and Davis, 1992; Peres, 1994; Harvey et al., 1987; Gaulin and Sailer, 1984; Strasser, 1992; Jungers, 1985). We rely mostly on the primary literature. We report data from secondary sources (e.g., Harvey et al., 1987) only when the source of primary data is not explicit and the body weight estimates clearly differ from those presented elsewhere. We employ only those sources that present separate data for males and females. We exclude data that are presented as only a range of weights. Sample sizes are provided where such information is available. All weights listed in Appendix A are taken from wild populations, and include only specimens that are reported as adult. Accordingly, the resulting data set of Appendix A is not an exhaustive compilation of all available weight data on anthropoid primates.

For each species (in Appendix A) we present data from different sources separately.

The pooling of data from different primary, or even secondary sources (e.g., Ford and Davis, 1992, Strasser, 1992) is justifiable on the grounds that increased sample sizes reduce standard errors of male and female body weight estimates, and consequently body weight dimorphism (e.g., see results of Plavcan, 1994). However, we avoid this practice for several reasons. First, differences in collection methods and evaluation criteria for what constitutes "adult" can confound attempts to merge data from different sources (Leigh, 1994). A good example is the orangutan, for which average "adult" male body weight (and consequently, the estimate of weight dimorphism) differs substantially depending on whether all sexually mature adult males are used, or only males that are sexually active (Markham and Groves, 1990).

Second, combination of body weight estimates from different secondary, and even sometimes primary sources can lead to redundancy if both sources use the same specimens. This is particularly likely to happen where primary data sources are not identified. For example, weight data for *Presbytis pileatus* (Appendix A) are cited from Oates et al. (1995), Green (1981), and Gaulin and Sailer (1984). Each source gives similar, but not identical, weight data because all rely at least in part on data provided by Oboussier and von Maydell (1959). Likewise, for *Presbytis obscurus*, Napier (1985) and Burtin (1981) give different weights, but Burtin (1981) notes that many of the specimens used for that study are housed in the British Museum (Natural History), making it likely that Napier's and Burtin's data are at least partly redundant.

Third, and perhaps most importantly, estimates of body weight and body weight dimorphism can vary dramatically if there is substantial intraspecific variation in body weight among populations or subspecies of a species. (e.g., see *Presbytis entellus*, *Cercopithecus aethiops*, *Cebus apella*, *Macaca nemestrina* in Appendix A). For example, variation in weight dimorphism among populations of *Cercopithecus aethiops* in Kenya ranges from 1.29 to 1.61 k (Turner et al., 1994). Size differences can be so substantial that pooling data from different populations can generate a biologically meaning-

less body weight estimate. For example, *Presbytis entellus* males from northern India are nearly twice as large as those from Sri Lanka. Averaging specimen data from these two regions both creates a body weight characteristic of neither population, and masks the enormous geographic variation in body weight of the species. Mixture of data for males from one region, and females from another (which is especially likely to happen with small sample sizes), can lead to a highly erroneous estimate of dimorphism.

For our analyses, we selected a single source of data for each species. For most species we selected the source with the largest sample size. Exceptions (noted in Appendix A) were made when a source indicated specifically that data were for a restricted population. Where several sources presented large sample sizes yielding a wide range of body weight estimates and body weight dimorphism (e.g., *Cercopithecus aethiops*), we used data that yielded intermediate values of dimorphism. In these cases, we re-evaluated our analyses to see whether variation in estimates of dimorphism would alter the results and conclusions.

Body size

We use female body weight as an estimate of overall size for evaluating the hypothesis that dimorphism allometrically increases with increasing overall body size (Leutenegger and Cheverud, 1982, 1985).

Body weight dimorphism

Interspecific variation in dimorphism can be produced by relative changes in either male or female traits. Ideally, a study should focus exclusively on male body size to test the sexual selection hypothesis. Recent studies of canine dimorphism successfully use this approach (Plavcan et al., 1995; Greenfield, 1992a,b; Smith, 1981). Unfortunately, because species differ both in body size and body size dimorphism, it is difficult to determine if dimorphism reflects a change in either male or female size, or a relative difference in either increase or decrease of both male and female body size. Martin et al. (1994) attempt to circumvent this problem by evaluating residual brain size and tooth size in males and females. However,

such indirect comparisons are highly tenuous (Smith, 1996). In particular, the interaction between body size and social behaviors predicted to be associated with the evolution of dimorphism (Plavcan and van Schaik, 1992; Plavcan et al., 1995; Mitani et al., 1996) can introduce substantial artifacts in an allometric analysis of dimorphism in male and female traits (Plavcan et al., 1995). Given this, we prefer to quantify dimorphism using a direct comparison of male to female body weight. The explicit assumption of this practice is that female body weight serves as a baseline of comparison to males (Plavcan and van Schaik, 1994).

We estimate dimorphism as the natural logarithm of the male mean body weight divided by the female mean body weight. This is equivalent to subtracting the natural logarithm of the female weight from that of the male, and substantially reduces skewness of the data (Gaulin and Sailer, 1984).

Several studies evaluate the relation between weight dimorphism and behavioral/ecological variables using residuals from a regression of body weight dimorphism against female body weight (Ford, 1994; Mitani et al., 1996; Martin et al., 1994). This practice is justifiable if there is an underlying allometric relation between overall body weight and body weight dimorphism (Leutenegger and Cheverud, 1982, 1985). The approach also helps to control for artifacts that may arise from the use of ratios (Ranta et al., 1994). However, this practice precludes evaluation of the hypothesis that correlations between body weight dimorphism and increasing body size reflect an interaction between body size and other behavioral/ecological variables (Mitani et al., 1996; Plavcan and van Schaik, 1992; Plavcan et al., 1995; Kappeler, 1990). Consequently, we rely primarily on the ln-transformed estimates of weight dimorphism for our analyses. Nevertheless, we repeated most of our analyses using residual estimates of body weight dimorphism from a least-squares regression of ln-transformed body dimorphism against ln-transformed female body weight.

Diet

We use two dietary classifications in this analysis. Following Plavcan (1990) and Plav-

can and van Schaik (1992), we employ five dietary categories (folivore, folivore/frugivore, frugivore/folivore, frugivore, and frugivore/insectivore). Species are classified as having mixed diets if the secondary component makes up greater than 15% (leaves or fruit) or 25% (insects) of the diet.

Additionally, because sample sizes vary among these dietary classifications, we collapse these categories into three broader dietary classes: folivorous, frugivorous, and frugivorous/insectivorous. Species are classified as folivorous or frugivorous if either of these components makes up greater than 50% of the diet. The frugivorous/insectivorous classification is retained.

Substrate

Following Plavcan and van Schaik (1992) and Plavcan et al. (1995), we recognize three substrate categories: arboreal, arboreal/terrestrial, and savanna-dwelling. Arboreal species are those that are reported as rarely or never descending to the ground. Arboreal/terrestrial species are those that spend at least some time on the ground, and some in the trees. Savanna-dwelling species are those that inhabit primarily open, savanna habitats.

Intrasexual competition

The most difficult aspect of testing the sexual selection hypothesis is measuring the strength of sexual selection associated with male-male agonistic competition. Ideally, variation in reproductive success should covary with those characters (e.g., large body size or weaponry) that are hypothesized to confer an advantage to individuals in winning contests. Such data are not available for most primates. Virtually all studies, therefore, assume that male-male contest competition is associated with variation in reproductive success, and attempt to estimate the degree of male-male competition in some way. Prior studies have used estimates of sex ratio (Clutton-Brock et al., 1977) or categorical estimates of mating system (Cheverud et al., 1985; Leutenegger and Cheverud, 1982, 1985; Gaulin and Sailer, 1984; Ely and Kurland, 1989; Kappeler, 1990). However, these estimates do not necessarily provide an accurate indication of

the degree of male-male competition (Mitani et al., 1996; Plavcan and van Schaik, 1992, 1994; Plavcan et al., 1995). Conversely, more theoretically precise estimates of male-male competition, such as the operational sex ratio, can be gleaned for only a relatively limited number of species (Mitani et al., 1996). This limits the scope of the analysis.

To estimate male-male agonistic competition, we use the "competition levels" of Plavcan and van Schaik (1992). The frequency and intensity of contests provide potentially independent pressures toward increased body size (Clutton-Brock, 1985). Quantitative data on the frequency and intensity of intermale aggression are rare. Nevertheless, it is possible to broadly estimate these two parameters using behavioral reports from the literature if we admit two assumptions: first that the intensity of intermale aggression is reflected by the observed tolerance among adult males towards each other, and second that the *potential* frequency of intermale aggression is a function of the proximity of males to each other (Plavcan, 1990; Plavcan and van Schaik, 1992).

We dichotomize intensity into a "high" and "low" class. *High-intensity* species are those where males are reported as intolerant of one another, where males are described as engaging in escalated combat, or where males form clear agonistic dominance hierarchies based on agonistic encounters. *Low-intensity* species are those where males are relatively tolerant of one another, where agonistic encounters are rare, or where dominance hierarchies either are absent, or are difficult to detect.

The potential frequency of male-male competition is also dichotomized into a "high" and "low" class. In those species where only a single adult male typically occurs in a breeding group (which we classify as *low-frequency*), agonistic competition is inevitably less frequent than in groups with more than one adult male (which we classify as *high-frequency*). In the former case, male-male competition is usually limited to occasional encounters with extragroup males, while in the latter case male-male competition can potentially occur on a daily basis. This classification of frequency is essentially a demographic measure of the number of

TABLE 1. Two-way ANOVA of the effects of intensity and frequency of male-male competition on *ln-transformed body weight dimorphism*¹

Effect	SS	DF	MS	F	P
Intensity	1.261	1	1.261	37.266	<0.001
Frequency	0.389	1	0.389	11.482	0.001
Interaction	0.001	1	0.001	0.036	0.850
Error	2.714	81	0.034		

¹ All anthropoids (N = 85).

males that typically occur in a breeding group, and really estimates the *potential*, rather than the actual, frequency of competition. However, we additionally classify as low-frequency those species where agonistic male-male competition is limited to a brief mating season (as in *Saimiri*, and in at least some populations of *Cercopithecus* in association with seasonal male influxes), even though more than one male may be present in a breeding group for some period of time.

As for canine dimorphism (Plavcan and van Schaik, 1992), a two-way analysis of variance (ANOVA) shows no significant interaction between the frequency and intensity classifications on body weight dimorphism (Table 1). Accordingly, the four combinations of frequency and intensity of male-male competition are ranked into "competition levels." For canine dimorphism, the effect of intensity is both theoretically and empirically greater than that of frequency (Plavcan, 1990; Plavcan and van Schaik, 1992; Plavcan et al., 1995). Thus, low-intensity male-male competition species are ranked into competition levels 1 and 2, and high-intensity male-male competition species are ranked into competition levels 3 and 4. The distinctions between levels 1 vs. 2, and 3 vs. 4, are between low-frequency and high-frequency classifications. This scheme predicts increase in dimorphism with increasing competition levels.

Classification of species into competition levels follows Kay et al. (1988) and Plavcan and van Schaik (1992), with the following changes. *Chiropotes satanas* is classified as competition level 2 (Ford, 1994). *Colobus guereza* is classified as competition level 4 (von Hippel, 1996). Finally, Plavcan and van Schaik (1992) had classified polyandrous *Saguinus* and *Leontopithecus* into competition level 1. However males of these species

should be classified as low-intensity, high-frequency competition (Plavcan et al., 1995), thus they are placed into competition level 2.

Monogamous species present a problem for the classification of species strictly on the basis of the frequency and intensity of male-male competition. Whereas males of *Callicebus* and *Callithrix* show low-intensity, low-frequency competition (competition level 1), both male and female *Hylobates* show high-intensity intersexual competition (Raemaekers and Raemaekers, 1985). Considered alone, male gibbons would be ranked as competition level 3 (Plavcan, 1993; Plavcan et al., 1995). However, in the case of pair-bonded species, even with the occasional extra-pair copulation, the correlation between the size of weaponry and reproductive success will necessarily be weaker than in non-monogamous species (Anderson, 1986; Clutton-Brock and Harvey, 1978; Emlen and Oring, 1977). Therefore, pair-bonded species are predicted a priori to show little or no dimorphism, whether or not males show intense competition (Anderson, 1994; Clutton-Brock and Harvey, 1978; Emlen and Oring, 1977; Darwin, 1871). Because competition level 1 species are predicted to show little or no dimorphism, we include all pair-bonded species in competition level 1. This fact should be kept in mind when evaluating our results.

Finally, Plavcan and van Schaik (1992) note that if dimorphism is measured as a ratio of male to female size, then the estimate of male-male competition should also account for male behavior relative to that of females. Plavcan et al. (1995) classify a number of anthropoid females as showing high-intensity female-female competition. It may be tempting to use the separate classifications of Plavcan et al. (1995) to predict degrees of dimorphism in anthropoids on the basis of both male and female intrasexual competition. This cannot be done. Male and female anthropoids usually compete for different resources—mates vs. food and safe positions. Consequently, since the reproductive consequences of winning contests are immediate and presumably also much greater for males than for females, selection associated with agonistic competition should be much greater in males than females.

Thus, for example, dimorphism is predicted in baboons, even though both males and females show intense intrasexual competition (Plavcan et al., 1995). The only clear exception to this is pair-bonded species. These distinctions should be kept in mind when comparing the results of this analysis and Plavcan and van Schaik (1992) to those of Plavcan et al. (1995).

Further details of the competition classifications and the justifications for them, are provided in Plavcan (1990, 1993), Plavcan and van Schaik (1992), and Plavcan et al. (1995).

Phylogeny

Following Plavcan et al. (1995), three complementary methods are used to control for the effects of phylogeny. First, within each genus an average of body weight dimorphism is taken for all species sharing similar behavioral or ecological classifications. This data set is referred to as the "generic-means data," and offers the advantage of preserving categorical information while reducing the effect of unbalanced representation of species among genera. Second, analyses are repeated within progressively lower taxonomic groups. This method allows independent tests of hypotheses within separate taxonomic groups, and controls for any gross differences between taxonomic groups in the expression of dimorphism. Finally, we use the "phylogenetic contrast" method of Felsenstein (1985).

To calculate phylogenetic contrasts, we employ the phylogenies used by Plavcan et al. (1995). For comparisons between quantitative characters such as body weight dimorphism and female body weight, we use the algorithm detailed in Pagel (1992), setting branch lengths equal to one (because most branch lengths are unknown). We resolve polytomies only where species can be grouped on the basis of competition levels. We carried out all calculations by hand. Where comparisons involve both categorical and quantitative characters, such as those between competition levels and body weight dimorphism, we used a modification of the procedure, described in detail in Plavcan et al. (1995). In short, we compare values of dimorphism between sister taxa (either species, or nodes) that differ in competition level. For all non-terminal nodes in the

phylogeny, we assign a competition level when all descendent taxa share the same competition level (exceptions to this are noted where appropriate). While it is possible to reconstruct nodes on the basis of parsimony (Maddison et al., 1984), we prefer to restrict tests of competition level only to those nodes where there is a relatively high degree of confidence in the behavioral reconstruction. We tabulate all the contrasts for each possible pair-wise comparison between competition levels. Finally, we use an ANOVA to test whether the absolute values of contrasts between taxa differing in competition level are significantly greater than those calculated between other nodes (that is, contrasts between nodes that either share the same competition level, or between nodes that were not assigned a competition level because of variation among descendent taxa in competition level).

We also use the phylogenetic contrast method to evaluate the relation between body weight dimorphism and female body weight. In this case, we calculated independent contrasts of body weight dimorphism and female body weight throughout the phylogeny without regard to competition level.

Statistics

For the categorical variables (competition levels, substrate, and diet), the effect of each category on dimorphism is not necessarily linear. For example, there is a greater difference in canine dimorphism between species of competition levels 1 and 2 than between other competition levels (Plavcan and van Schaik, 1992). For this reason, we prefer non-parametric statistics for comparisons of these categorical variables to body weight dimorphism. Nevertheless, we also carried out parametric tests for all analyses. Results are the same in almost all cases. We carried out all statistical analyses using the SYSTAT program (version 5.02, Wilkinson, 1990).

Because we make a large number of statistical comparisons, the likelihood that significance results represent Type I errors is increased for each analysis. Therefore, we present both "unprotected" significance levels in our results, as well as Dunn-Sidak adjusted probabilities (in all cases based on an unprotected significance level of 0.05). The

Dunn-Sidak method adjusts probabilities on the basis of the number of tests carried out for each analysis (Sokal and Rohlf, 1995).

RESULTS

Phylogeny

ANOVA shows significant differences in the degree of dimorphism among different families and subfamilies of anthropoids ($N = 86$, $F = 15.841$, $P < 0.001$ for analysis of the 8 groups shown in Fig. 2). On average, cercopithecines show the greatest degree of dimorphism, while callitrichines, pitheciines, and hylobatids show consistently low levels of dimorphism (Fig. 2). However, there is a broad range of dimorphism within aotines, colobines, atelines, great apes, and cercopithecines, with extensive overlap in the range of dimorphism among them.

Competition

Using the data set of all anthropoids, the Spearman rank correlation between competition levels and body weight dimorphism is in the predicted direction (Table 2), with increasing competition level associated with increasing body weight dimorphism (Fig. 3). This result obtains for the taxonomically controlled data, within lower taxonomic groupings, and also using residuals from a regression of body weight dimorphism on female body weight.

These results are corroborated by Mann-Whitney U-tests for pair-wise comparisons between species of different competition levels (Table 3). All comparisons are in the predicted direction (higher competition levels show higher average dimorphism), and all are highly significant using unprotected significance levels. Comparisons between competition levels 1 and 2, and levels 3 and 4 are not significant using Dunn-Sidak protected probabilities. The generic-means data show a similar result, except that the comparison between competition levels 3 and 4 is not significant. These results are generally repeated within lower taxonomic groups. Within lower taxonomic groups, distinctions between levels 1 and 2, and 3 and 4, respectively, are for the most part not significant, though the differences in average dimorphism between competition levels are always in the predicted direction. Thus, within

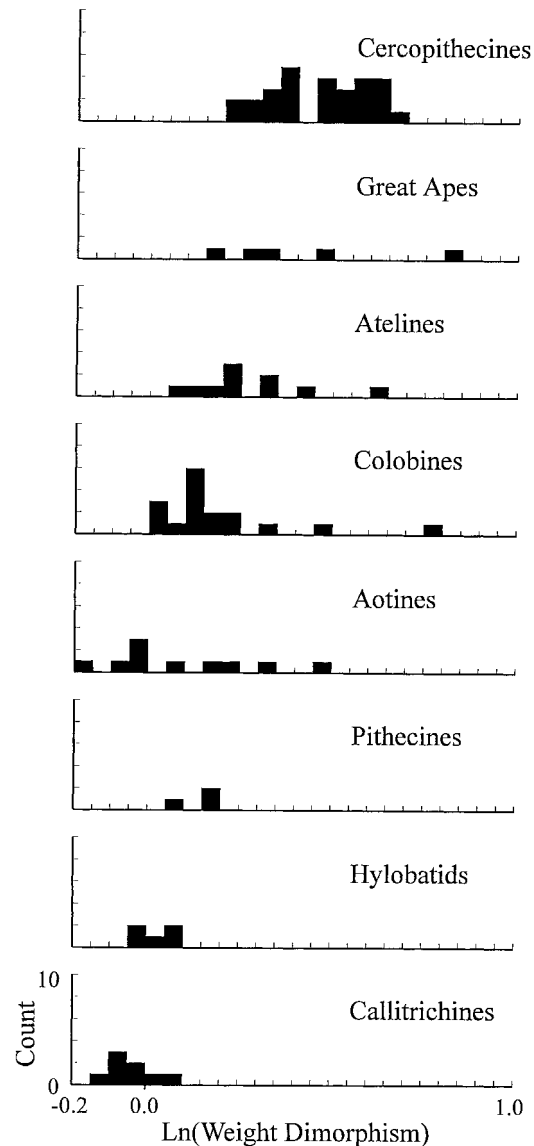


Fig. 2. Frequency histograms of ln-transformed body weight dimorphism estimates among families and subfamilies of anthropoid primates. Axes are the same for each histogram. "Great apes" refers to species of *Pan*, *Gorilla* and *Pongo*. "Aotines" refers to *Callicebus*, *Aotus*, *Saimiri*, and *Cebus*.

lower taxonomic groups the evidence for the potential frequency effect is weak at best using species values. These results recur using residuals from a regression of body weight dimorphism on female body weight.

Phylogenetic contrasts are in the predicted direction for all but one case (Table 4).

TABLE 2. Spearman rank correlations between competition level and \ln -transformed body weight dimorphism for the entire sample, and within lower taxonomic groups

Group	N	Rs	P*
All	85	0.731	<0.001
Catarrhines	54	0.518	<0.001
Platyrrhines	31	0.850	<0.001
Cercopithecoids	45	0.420	0.002
Hominoids	9	0.904	<0.001
Ceboids	23	0.908	<0.001
Colobines	17	0.762	0.017
Atelines	10	0.853	0.029
Aotines	10	0.849	0.001
Generic means	35	0.805	<0.001

* Probabilities are for a parametric Pearson's product-moment correlation, a close approximation recommended by Sokal and Rohlf (1995) for the Spearman rank correlation. Only groups for which 3 or 4 competition levels are represented are evaluated. Protected level of significance is 0.005.

This exception (*Cercopithecus aethiops* vs. other *Cercopithecus*) involves a contrast between competition levels 3 and 4, reflecting a difference in the frequency classification of male-male competition. Four contrasts listed in Table 4 (including the negative contrast) can be reversed in sign by selecting alternative body weight data from Appendix A. ANOVA shows that phylogenetic contrasts listed in Table 4 [using only contrasts from the Ford (1986) phylogeny for platyrrhines in order to avoid redundancy] are significantly greater than other contrasts ($N = 50$, $F = 7.298$, $P = 0.005$ for a one-tailed test). Using alternative phylogenies for platyrrhines does not alter this result.

Regarding taxonomic correlations of weight dimorphism, when colobines are removed from the analysis, there is less overlap in the distribution of high-intensity (competition levels 3 and 4) and low-intensity (competition levels 1 and 2) species (Fig. 3). In particular, within competition level 3, colobines show significantly less weight dimorphism than other cercopithecines or anthropoids (Table 5). In fact, colobines produce much of the overlap in the range of dimorphism of competition level 3 with competition levels 1 and 2. This is shown in Figure 3, which shows frequency histograms of body weight dimorphism within competition levels for the entire anthropoid sample, for non-colobine anthropoids, and for colobines. Among non-colobine anthropoids, the distinction between high-intensity (competi-

tion levels 3 and 4) and low-intensity (competition levels 1 and 2) species is better defined than when the two groups are combined. These observations are not altered by variation in reported values of weight dimorphism for colobine species. Furthermore, a similar pattern of results is not produced when other families or subfamilies are removed from the analysis, even though there are obvious differences among families and subfamilies in the average degree of body weight dimorphism (Fig. 2).

Female body weight

Among all anthropoid primates, there is a significant, positive correlation between female body weight and body weight dimorphism (Table 6). This result is repeated for the generic-means data, and using phylogenetic contrasts. Within lower taxonomic groups, the platyrrhines, hominoids, and cercopithecines yield correlations between female body weight and body weight dimorphism that approach "unprotected" significance levels. However, only among platyrrhines is the correlation significant using the Dunn-Sidak protected significance level.

There is some evidence to suggest that significant correlations between female body weight and body weight dimorphism might reflect an interaction between overall body size and competition levels. Overall, there is a significant correlation between increasing competition levels and increasing female body weight ($r_s = 0.357$, $N = 86$, $P < 0.001$). Within competition levels 1 and 3, correlations between female body weight and body weight dimorphism are not significant (Table 6). Within competition level 4 the correlation is significant using an "unprotected" significance level, but not using a Dunn-Sidak protected significance level. Only within competition level 2 is the correlation clearly significant. Scrutiny of the phylogenetic contrasts provides some support for this hypothesis. As noted above, phylogenetic contrasts calculated between nodes differing in competition levels are significantly greater than those calculated between other nodes. Within these two groupings of contrasts, the correlation between weight dimorphism and female body weight is either weak or non-significant (contrasts

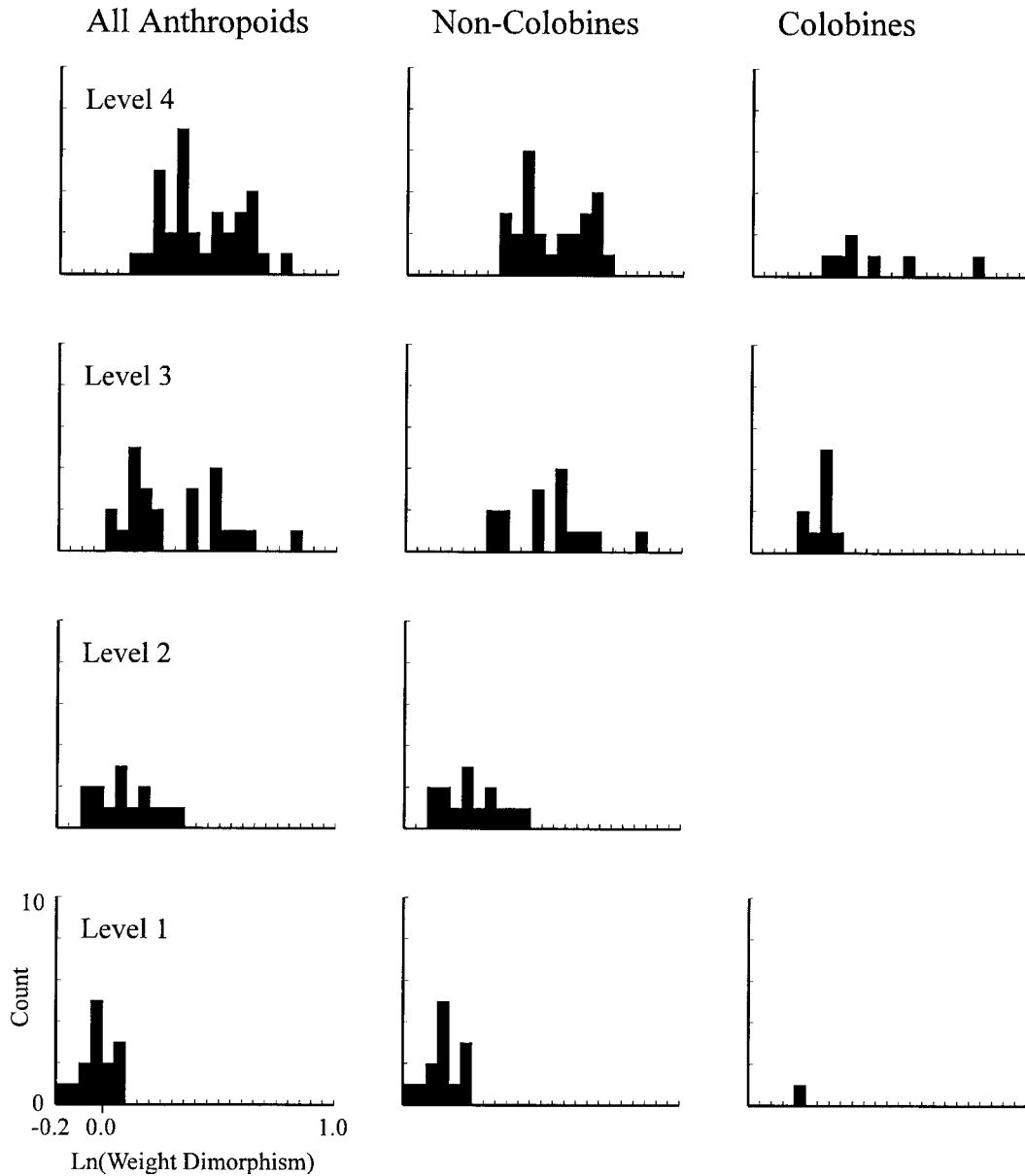


Fig. 3. Frequency histograms of ln-transformed body weight dimorphism estimates among species of each competition level for all anthropoids, non-colobine anthropoids, and colobines. Axes are the same for each histogram.

between competition levels: $N = 13$, $r = 0.546$, $P = 0.043$; other contrasts: $N = 37$, $r = 0.216$, $P = 0.139$).

Substrate

Across all anthropoids, there are significant differences in body weight dimorphism

between the substrate classifications, with arboreal species showing lower levels of dimorphism than either arboreal/terrestrial or savanna-dwelling species (Table 7, Fig. 4). This result may in part reflect an interaction between competition levels and substrate classifications—most competition level

TABLE 3. Mann-Whitney U-tests for pair-wise comparisons of body weight dimorphism between species of different competition levels for all anthropoids, and for generic-means data¹

	Level 1	Level 2	Level 3
All anthropoids			
Level 2			
U	45.5	—	
n	14/14		
P	0.009		
Level 3			
U	9.5	84.0	—
n	14/24	14/24	
P	<0.001	0.004	
Level 4			
U	0.0	22.5	235.0
n	14/33	14/33	24/33
P	<0.001	<0.001	0.012
Generic means data			
Level 2			
U	6.0	—	
n	7/8		
P	0.011		
Level 3			
U	1.0	11.0	—
n	7/8	8/8	
P	0.002	0.027	
Level 4			
U	0.0	1.0	38.0
n	7/12	8/12	8/12
P	<0.001	<0.001	N.S.

¹ Sample sizes listed below the values of U are for the competition levels listed in the columns and rows, respectively. Protected level of significance for each analysis is 0.008.

1 species are arboreal. Within competition levels, differences in dimorphism between substrate categories are significant in four of seven comparisons using unprotected significance levels, but none of these are significant using Dunn-Sidak protected significance levels (Table 7). Two of the three non-significant results involve small sample sizes. These results recur for the generic-means data, within lower taxonomic groups, and using residuals of weight dimorphism derived from a regression of body weight dimorphism on female body weight. There are too few phylogenetic contrasts to evaluate and control for interactions with competition levels.

Diet

Using the five-part dietary classification, there are no significant differences between dietary classifications for 8 of 10 comparisons using the anthropoid sample as a whole. Significant differences are found between folivore/frugivores and frugivores (Mann-Whitney U = 71.00, n = 18 vs. 17, $P = 0.007$),

and between frugivores and frugivore/insectivores (Mann-Whitney U = 127.00, n = 17 vs. 9, $P < 0.001$). In both cases, the frugivorous species show greater average dimorphism than species of the other dietary classification. Comparisons within lower taxonomic groups and competition levels are precluded by small sample sizes.

Using the "collapsed," tripartite dietary divisions (recognizing only folivores, frugivores, and frugivore/insectivores), frugivores show significantly different dimorphism than frugivore/insectivores using "unprotected" significance levels, but not using Dunn-Sidak protected significance levels (Table 8, Fig. 5). Within competition levels, frugivores differ significantly in weight dimorphism from folivores within competition levels 3 and 4, and from frugivore/insectivores in competition level 2. None of these latter comparisons is significant using Dunn-Sidak protected significance levels. Most of the non-significant results involve comparisons with small sample sizes.

Regardless of significance levels, we find that folivores on average show less dimorphism than frugivores. This result is the opposite direction to that found by Ford (1994) for platyrrhines, and partly reflects the low degrees of weight dimorphism exhibited by colobines.

DISCUSSION

Male-male competition, sexual selection and body weight dimorphism

Our results demonstrate a strong link between male-male competition and the magnitude of body weight dimorphism in anthropoid primates, supporting the hypothesis that sexual selection via the mechanism of male-male competition plays an important role in the evolution of body weight dimorphism.

The consistent, strong distinction in weight dimorphism between competition levels 1 and 2 (low-intensity male-male competition), and 3 and 4 (high-intensity male-male competition) supports the hypothesis that larger size confers an advantage to males in intrasexual combat for access to females. High-intensity species (competition levels 3 and 4) are characterized by intense male-male competition for access to mates,

TABLE 4. Standardized phylogenetic contrasts of Ln-transformed body weight dimorphism between species or nodes differing in competition levels¹

Contrast	1 vs. 2	2 vs. 3	3 vs. 4	1 vs. 3/4	2 vs. 4	Reference
<i>Saguinus</i> vs. <i>Cebuella/Callithrix</i>	0.030					Kay (1990)
<i>Leontopithecus</i> vs. <i>Cebuella/Callithrix</i>	0.090					Ford (1986)
<i>Aotus</i> vs. <i>Pithecinini</i>	(0.081)					Rosenberger (1979, 1981). Assumes ancestral pithecini was competition level 2
<i>Gorilla gorilla</i> vs. <i>Pan</i>		0.109				
<i>Pithecia pithecia</i> vs. <i>Cacajao calvus</i> ²		0.006				Ford (1986)
<i>Chiropotes satanas</i> vs. <i>Cacajao calvus</i> ²		0.074				Kay (1990), Rosenberger (1979, 1981)
<i>Cercopithecus aethiops</i> vs. other <i>Cercopithecus</i>			-0.043			
<i>Colobus angolensis</i> vs. <i>C. guereza</i>			0.029			
<i>Semnopithecus entellus</i> vs. <i>Kasi</i>			0.181			
<i>Cebus apella</i> vs. <i>Saimiri</i> ²			0.017			
<i>Nasalis larvatus</i> vs. presby- tines			(0.242)			Assumes ancestral presby- tine was competition level 3
<i>Cercopithecines</i> vs. papio- nines			(0.022)			Assumes ancestral cercopi- thecines were competi- tion level 3
<i>Presbytis potenziani</i> vs. <i>P. melalophosgroup</i> ²				0.008		
<i>Saimiri</i> vs. <i>Aotus/Calli- cebus</i>				0.147		Ford (1986)
<i>Saimiri</i> vs. callitrichines				0.123		Kay (1990)
<i>Hylobatids</i> vs. great apes				(0.236)		Assumes ancestral great ape was not competition level 1
<i>Alouatta</i> vs. other atelines					0.088	Ford (1986)
<i>Alouatta</i> vs. other atelines					0.085	Rosenberger (1979, 1981)
<i>Alouatta</i> vs. <i>Brachyteles arachnoides</i>					0.124	Kay (1990)
<i>Cebus</i> vs. other platyr- rhines					0.068	Ford (1986). Assumes that the ancestor of "other" platyrrhines was not competition level 4
<i>Cebus</i> vs. other platyr- rhines					0.060	Kay (1990). Assumes that the ancestor of "other" platyrrhines was not competition level 4

¹ Columns list the competition levels contrasted. Contrasts are calculated so that a positive value corroborates the competition hypothesis. Contrasts in parentheses are based on reconstructed competition levels for higher nodes.

² Sign of contrast changes depending on which weight data are used.

with large reproductive advantages presumably conferred to those males capable of winning fights with conspecific males. The presence of high degrees of dimorphism in these species is thus consistent with the sexual selection hypothesis.

Conversely, the low degrees of weight dimorphism in low-intensity species does not necessarily imply either a lack of sexual selection or a lack of male-male competition. On the one hand, several species classified in competition levels 1 and 2 are indeed

characterized by relatively little overt male-male competition for access to females (e.g., *Callicebus*, *Brachyteles*). On the other hand, there is evidence for male-male competition for access to females in, for example, hylobatids (e.g., Palombit, 1993). The large male canine teeth of these species are consistent with this observation (Plavcan, 1993; Plavcan et al., 1995). However, female hylobatids also have been observed to aggressively defend their territories, like males (e.g., Raemaekers and Raemaekers, 1985). Large fe-

TABLE 5. ANOVA comparing body weight dimorphism of colobines to other cercopithecoids and anthropoids of competition level 3

Effect	SS	DF	MS	F	P*
Competition level 3					
Colobines vs. cerco- pithecines (N = 18)					
Group	0.537	1	0.537	57.014	<0.001
Error	0.151	16	0.009		
Colobines vs. anthropoids (N = 24)					
Group	0.585	1	0.585	28.321	<0.001
Error	0.454	22	0.021		

* Probability for a one-tailed test. Protected significance level is 0.025.

TABLE 6. Pearson's product-moment correlation of In-transformed body weight dimorphism with In-transformed female body weight in all anthropoids, within a series of lower taxonomic groups, for phylogenetic contrasts, and within competition levels

Group	N	r	P*
All anthropoids	85	0.517	<0.001
Catarrhines	54	0.175	N.S.
Platyrrhines	31	0.612	<0.001
Cercopithecoids	45	0.121	N.S.
Hominoids	9	0.817	0.007
Ceboids	23	0.384	N.S.
Callitrichids	8	0.484	N.S.
Cercopithecines	28	0.439	0.019
Colobines	17	0.456	N.S.
Pongids	4	0.202	N.S.
Hylobatids	5	0.008	N.S.
Atelines	10	0.458	N.S.
Aotines	10	0.152	N.S.
Callitrichines	8	0.484	N.S.
Pitheciines	3	0.346	N.S.
Generic means	35	0.653	<0.001
Phylogenetic contrasts ¹	50	0.374	0.007
Competition levels			
Level 1	14	0.520	N.S.
Level 2	14	0.888	<0.001
Level 3	24	0.177	N.S.
Level 4	33	0.374	0.032

¹ Sample size of the contrasts is only 50 due to unresolved polytomies in the phylogenies. Analysis uses the Ford (1986) phylogeny for platyrrhines.

* Protected level of significance for the analyses within taxonomic groups is 0.003. Protected level of significance for the analysis within competition levels is 0.013.

male canines are consistent with this behavior, and the slight canine dimorphism exhibited by all hylobatids is consistent with the hypothesis that selection for the development of weaponry is broadly similar in both sexes (Plavcan et al., 1995). It follows that the low degree of body weight dimorphism characterizing all hylobatids (and all monogamous species) is, like the canines, not necessarily indicative of an absence of sexual

TABLE 7. Mann-Whitney U-tests between substrate classifications for all anthropoids, and within competition classifications

	All	Comp 1	Comp 2	Comp 3	Comp 4
Contrast ¹					
A vs A/T					
U	187.5	—	0.0	29.0	45.5
n	58/21		12/2	17/6	15/13
P	<0.001		0.028	N.S.	0.017
A vs S					
U	15.0	—	—	1.0	8.0
n	58/6			17/1	15/5
P	<0.001			N.S.	0.010
A/T vs S					
U	16.0	—	—	0.0	12.0
n	21/6			6/1	13/5
P	0.006			N.S.	0.043

¹ Protected level of significance for all comparisons is 0.005.

selection, but rather a lack of sex differences in selection for larger body size associated with intrasexual competition.

Several species classified in competition level 2 (e.g., chimpanzees) show relatively low intensity male-male competition within groups, but potentially intense male-male competition between groups. Plavcan et al. (1995) demonstrate that when escalated agonistic intrasexual competition typically occurs between groups of individuals, rather than between two individuals fighting alone, selection for the development of weaponry is probably not very strong. A similar mechanism may operate for body weight dimorphism. However, the demonstration of this effect is contingent on partitioning male and female components of dimorphism (Plavcan et al., 1995). Such an analysis is beyond the scope of this paper.

The evidence for a relation between weight dimorphism and the potential frequency of male-male competition is much weaker than that for a relation between weight dimorphism and the intensity of male-male competition. Ford (1994) found no relation between the frequency classification and weight dimorphism in platyrrhines. Our data set yields the same result for platyrrhines. However, phylogenetic contrasts involving the frequency classification are all in the predicted direction with only one exception, while analysis of the entire sample and the generic means data provides weak evidence in support of a frequency effect. Plavcan and van Schaik (1992) suggest that the relation

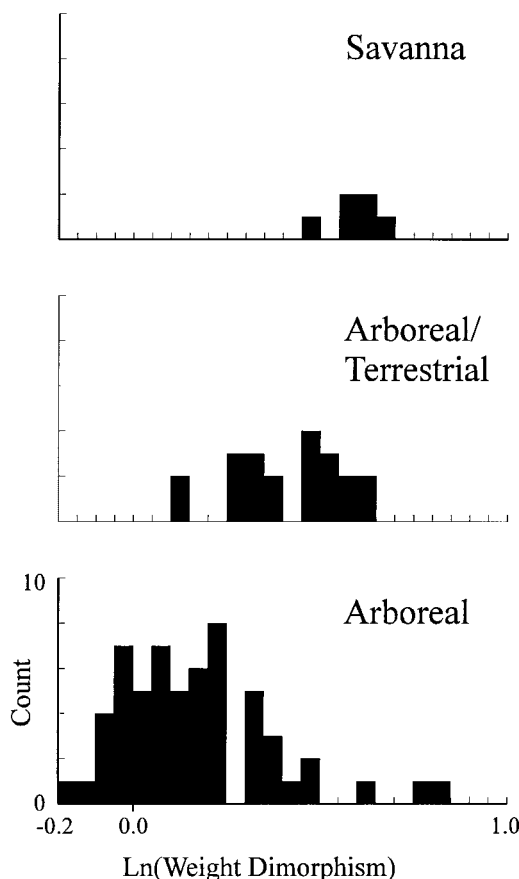


Fig. 4. Frequency histograms of ln-transformed body weight dimorphism for anthropoids within different substrate classifications. Axes are the same for each histogram.

between the frequency classifications and canine dimorphism reflects not an actual increase in the frequency of use of the canines for inflicting wounds, but rather selection for weapons as display items. This is predicted on the hypothesis that, if several males living together in a group are basically intolerant of one another, then escalation of a conflict into a potentially damaging fight could be physically detrimental to the contestants, but not to non-participant males. Therefore, escalation of contests actually could benefit non-participant males. If so, selection should favor the development of weapons for deciding the outcome of contests through display (backed up, of course, by the actual threat to escalate). A similar

TABLE 8. Mann-Whitney U-tests between diet classifications for all anthropoids, and within competition levels

	All	Comp 1	Comp 2	Comp 3	Comp 4
Contrast ¹					
Folivore vs. frugivore					
U	326.0	10.0	2.0	15.0	31.0
n	22/44	2/8	1/6	9/12	10/18
P	0.032	N.S.	N.S.	0.006	0.005
Folivore vs. insectivore					
U	188.5	4.0	6.0	1.0	3.0
n	22/12	2/2	1/7	9/2	10/1
P	0.042	N.S.	N.S.	N.S.	N.S.
Frugivore vs. insectivore					
U	402.5	12.0	39.0	5.0	15.0
n	44/12	8/2	6/7	12/2	18/1
P	0.006	N.S.	0.010	N.S.	N.S.

¹ Protected level of significance for all comparisons is 0.004.

explanation has been put forward for the evolution of large antlers and horns in ungulates (Geist, 1965). If true, our results suggest that selection does not strongly favor increased male body weight for display. This, in turn, suggests either that body weight is a comparatively expensive trait to enhance for display purposes, by comparison to increasing canine size, or that increased body size is relatively less intimidating to opponents than are canines.

Our analysis suggests that the long-standing observation that many polygynous anthropoids show low degrees of body weight dimorphism, in apparent contradiction to the sexual selection hypothesis (Martin et al., 1994), is at least partly an artifact of two factors: first, a poor relation between behavioral classifications of mating system and variation in male-male competition and, second, inadequate evaluations of phylogenetic patterns of weight dimorphism.

A number of studies have noted that the classification of "polygyny" commonly used in studies of size dimorphism masks substantial variation in the intensity of male-male competition (Mitani et al., 1996; Plavcan and van Schaik, 1992, 1994; Plavcan et al., 1995). The competition levels in this analysis recognize that polygynous species of competition level 2, such as *Pan*, *Ateles*, and *Brachyteles*, are not characterized by very intense male-male competition for access to

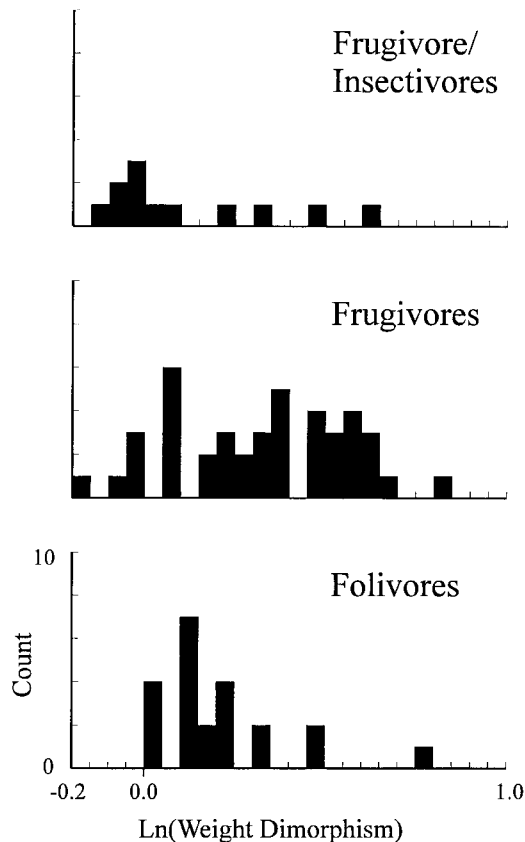


Fig. 5. Frequency histograms of ln-transformed body weight dimorphism for anthropoids within the tripartite ("collapsed") diet classifications. Axes are the same for each histogram.

mates by comparison to species typical of competition levels 3 and 4. Excluding monogamous and polyandrous species from the analysis, competition levels are still significantly associated with variation in weight dimorphism ($N = 65$, $F = 6.091$, $P = 0.004$, see also phylogenetic contrasts in Table 4).

Further support for this suggestion is provided by Mitani et al. (1996), who find a strong relation between weight dimorphism and the operational sex ratio across 18 anthropoid species. Notably, 14 of the species used by Mitani et al. (1996) are classified by us as competition level 4, practically meaning that their study offers a narrow analysis of male-male competition within a single competition level (re-analysis of Mitani et al.'s data using only competition level 4

species does not alter their result). The relation between weight dimorphism and operational sex ratio found in Mitani et al.'s study suggests that our competition levels also mask interspecific variation in male-male competition, and consequently the strength of sexual selection (Plavcan, 1993; Plavcan et al., 1995). Thus, at least some of the variation in dimorphism within competition levels may reflect unquantified variation in male-male competition.

On the other hand, this conclusion should be tempered by the observation that Mitani et al.'s (1996) results change depending on the weight data used in the analysis. We re-analyzed Mitani et al.'s (1996) data following their methods and phylogeny. The analyses differed primarily in that we did not calculate a contrast for the *Alouatta* trichotomy. Recalculation of the contrasts using their data yields similar results ($N = 15$, $r = 0.811$, $P < 0.001$). However, using weight data from Appendix A, there is no significant correlation between contrasts ($N = 15$, $r = 0.395$, $P = 0.130$).

The wide range of dimorphism seen among polygynous primates is further explained by a second observation—that among polygynous primates, colobines as a group show very little weight dimorphism (Leutenegger and Kelley, 1977). Among non-colobine anthropoids, there is comparatively little overlap in the range of body weight dimorphism between high-intensity and low-intensity male-male competition species. The low levels of colobine weight dimorphism by comparison to other anthropoids offer an interesting problem for understanding the evolution of body weight dimorphism (see below, Phylogeny).

Female body weight

That body size dimorphism tends to be greater in larger anthropoids is widely acknowledged. However, the mechanisms governing the relation between overall body size and body weight dimorphism are widely debated. For example, Leutenegger and Chaverud (1982, 1985) offer a quantitative genetic model, which predicts that if male traits are either less heritable, or more variable than female traits, then dimorphism will evolve simply as a consequence of

increasing overall body size. Ford (1994) offers data suggesting that there is no allometric relation between body size and body weight dimorphism in platyrrhines. Mitani et al. (1996) suggest that correlations between body size and body weight dimorphism reflect an interaction between overall size and operational sex ratios. Studies of canine dimorphism (Plavcan and van Schaik, 1992; Plavcan et al., 1995) also suggest that correlations between dimorphism and body weight reflect an interaction between overall size and male-male competition. Kappeler (1990) suggests that selection for increased male body size is decoupled from male-male competition below a certain body size threshold.

Considered alone, the broad correlation between female body weight and body weight dimorphism is consistent with the hypothesis that body weight dimorphism is at least partly an allometric consequence of increasing female body weight (Leutenegger and Cheverud, 1982, 1985). However, our results support the conclusions of Kappeler (1990, 1991), Godfrey et al. (1993), Ford (1994), and Mitani et al. (1996), that increasing body weight dimorphism is not a direct, allometric consequence of increasing overall body size. Rather, the overall correlation between weight dimorphism and increasing female body weight reflects interactions between behavior and body size, as suggested by Mitani et al. (1996) and Kappeler (1990, 1991). Similar results are obtained for canine dimorphism by Plavcan and van Schaik (1992). Mitani et al. (1996) suggest that a correlation between female body size and female reproductive rates may generate the correlation between body weight dimorphism and overall body size. Thus, in larger species, females show longer intervals between estrous cycles, and longer interbirth intervals. This leads to male-biased operational sex ratios, which leads to more intense competition between males for access to females.

Phylogeny

Body weight dimorphism is clearly correlated with taxonomy, supporting the hypothesis of Cheverud et al. (1985) that phylogenetic factors play an important role in the

evolution of primate dimorphism. The exact mechanisms underlying these taxonomic correlations, however, are debatable and probably differ from taxon to taxon. For several taxa, such as hylobatids, callitrichids, *Cercopithecus*, and *Macaca*, all species are characterized by broadly similar types of intrasexual competition, and similar degrees of body weight dimorphism. The consistent relation between competition levels and body weight dimorphism within most families and subfamilies suggests that stabilizing selection maintains dimorphism in species sharing similar behavioral repertoires (Plavcan and van Schaik, 1992; Plavcan 1993). In this sense, these taxonomic correlations appear to reflect "phylogenetic niche conservatism" as suggested by Harvey and Pagel (1991). Conversely, the low levels of body weight dimorphism shown by colobines appear to reflect some mechanism constraining dimorphism in this group.

Leutenegger and Kelly (1977) first noted that, among polygynous anthropoids, colobines as a group show low degrees of body weight dimorphism. This does not appear to be associated with a lack of male-male competition (Leutenegger and Kelly, 1977). To the contrary, males of some colobine species fight very aggressively for access to females (e.g., Kunkun, 1986; Rudran, 1973). Furthermore, most colobines show substantial canine dimorphism, consistent with our classification of most colobines in competition levels 3 and 4 (Plavcan and van Schaik, 1992). Low levels of body weight dimorphism could result either from some factor limiting the development of large male body weight, or some factor that favors a relative increase in female body size.

Leutenegger and Kelly (1977) first suggested that energetic constraints associated with a folivorous diet limit the development of male body weight in highly active, arboreal colobines. However, neither arboreality nor folivory is strictly correlated with low degrees of weight dimorphism. A number of arboreal species are larger and more dimorphic than colobines. Several folivorous species, including some colobines (e.g., *Nasalis larvatus*, *Presbytis entellus*), are highly dimorphic. Demment (1983) suggested that metabolic considerations, coupled with po-

tential competition from herbivorous ungulates, might place an upper limit on the development of male body size in baboons. However, this model was developed to explain why baboons, which already show very high degrees of body weight dimorphism, are not even more dimorphic. Thus, Demment's (1983) model cannot be invoked to explain the colobine pattern of dimorphism in terms of an upper limit on male body size.

We are aware of little evidence that ontogeny can explain the colobine pattern of dimorphism. Folivorous anthropoids tend to increase in body size through rate hypermorphosis, showing relatively little bimaturism and early maturity compared to non-folivorous species (Leigh, 1992, 1995). High rates of growth in both males and females coupled with relatively little bimaturism might leave little room for the development of body weight dimorphism. However, there is no relation between the degree of dimorphism and the *proportion* of weight dimorphism that is achieved through an increased rate of male growth (Leigh, 1992). Several species showing relatively high rates of male body weight growth (*Presbytis entellus*, *Erythrocebus patas*, *Gorilla gorilla*, half the sample analyzed by Leigh, 1995) also show high degrees of body weight dimorphism (Leigh, 1995).

Conversely, the low levels of body weight dimorphism in colobines might reflect some factor that favors relatively large females. The fact that several species show high degrees of body weight dimorphism (e.g., *Nasalis*, *Presbytis entellus*) suggests that the low dimorphism characteristic of most colobines does not reflect a genetic linkage between male and female body size (Lande, 1980). Following Ralls' (1976) hypothesis that increased female body size reduces the metabolic costs of pregnancy, low levels of dimorphism might reflect selective pressure to increase female body size in folivorous primates that subsist on a relatively low energy, folivorous diet. This might be coupled with the well-known strategy of mammalian folivores to increase digestive efficiency by slowing gut-passage time (Demment, 1982, 1983, Demment and van Soest, 1983). However, several folivorous primates (including *Nasalis larvatus* and *Presbytis entellus*) show

substantial levels of body weight dimorphism. Therefore, we can offer no compelling explanation for the pattern of colobine weight dimorphism. However, understanding the evolution of weight dimorphism in this group should provide substantial insight into mechanisms governing the evolution of dimorphism in all primates.

Substrate

Two hypotheses predict that highly arboreal species should show less weight dimorphism than more terrestrial species. First, larger male body size might confer an advantage to males for defense from large-bodied terrestrial predators (Anderson, 1986; Clutton-Brock et al., 1977; Leutenegger and Kelly, 1977). Second, arboreality might place an upper limit on male body weight (Clutton-Brock et al., 1977) if large body size is a detriment to movement in an arboreal environment. Note that both hypotheses make the same predictions about the relation between size dimorphism and the substrate classifications used in our analysis.

We find weak evidence in support of these two hypotheses. It is clear that, across all anthropoids, arboreal/terrestrial species show greater weight dimorphism than strictly arboreal species. However, close scrutiny of our results suggests that the relation between substrate and weight dimorphism in anthropoids may reflect an interaction between substrate classifications and competition levels. Environmental conditions may influence male-male competition in several ways. First, terrestrial groups are often larger, making them more likely to contain multiple males and thus to produce high-frequency competition. Second, for arboreal males speed and agility in moving about a three-dimensional environment may partly offset advantages in winning contests from increased body size. Third, arboreal species are, on average, smaller than terrestrial species. As discussed above, there appears to be an association between larger size and increased male-male competition. Thus, while we cannot rule out substrate constraints or predation pressure as causal factors explaining the relation between substrate and dimorphism, other explanations are plausible.

Finally, more subtle relations between substrate and weight dimorphism are possible. Our substrate classifications are very broad, and in particular, do not distinguish between locomotor types. For example, arboreal species may be vertical clingers and leapers, arboreal quadrupeds, suspensory, etc. Different modes of locomotion may have different effects and relationships with body size that may or may not affect weight dimorphism. Such an analysis is beyond the scope of this paper.

Diet

Several hypotheses make conflicting predictions about the relation between diet—particularly folivory—and weight dimorphism in anthropoid primates. Milton (1985) suggests that the low-energy diet of folivores constrains the expression of male-male competition. Hence, folivores should be less dimorphic than other species. Leutenegger and Kelly (1977) suggest that a low-energy folivorous diet may produce selection to limit male body size in highly active arboreal species. Conversely, Ford (1994) and Mitani et al. (1996) suggest on the basis of energetic considerations that the fitness consequences of becoming larger should be lower in folivores than in frugivores, allowing the development of relatively larger male size and size dimorphism in folivorous species.

We find weak evidence for a relation between body weight dimorphism and diet. On average, frugivorous species show greater dimorphism than either folivores or frugivore/insectivores (contra Ford, 1994, and Mitani et al., 1996). This latter comparison might reflect an interaction between overall size, diet, and intrasexual competition. Most species that include a large number of insects in their diet are small and ranked into competition levels 1 and 2. Within competition levels, most comparisons between frugivore/insectivores and other species are non-significant.

Our results contradict those of Ford (1994), who found that folivorous platyrrhines show significantly higher levels of body weight dimorphism than species of other dietary guilds. This difference is not the result of different schemes for classifying diet. While Ford uses a more refined classification of

dietary guilds than ours, our classification of folivores is largely compatible. All but one of the folivores listed by Ford are species of *Alouatta*, all of which are characterized by high-intensity male-male competition. *Brachyteles*, the only other folivorous species listed by Ford, is characterized by dimorphism consistent with other competition level 2 species.

We are unable to evaluate Ford's finding that soft-fruit eaters show less dimorphism than species of other dietary guilds.

We emphasize that our dietary classifications are broad, masking more subtle variations in diet that may be linked to dimorphism (Ford, 1994; Plavcan et al., 1995). Grouping patterns and social behavior are related to diet, hence, intrasexual competition ultimately should be associated with diet (Plavcan et al., 1995). For example, Ford (1994) notes that insectivory is associated with female dispersal patterns resulting in monogamy and polyandry. We anticipate that more detailed comparative analyses will reveal clearer links between diet and size dimorphism.

Factors not addressed in this analysis

Our analysis addresses neither the hypothesis that variation in adult dimorphism is associated with variation in the ontogeny of dimorphism (Shea, 1986; Leigh, 1992, 1995; Leigh and Shea, 1994), nor the hypothesis that differing male and female life history strategies result in selection for different male and female body size (Ford, 1994; Martin et al., 1994). Regarding ontogeny, Leigh (1992) demonstrates that variation in ontogenetic pathways producing dimorphism does not appear to constrain the magnitude of adult dimorphism. With reference to the life-history hypotheses, Ford (1994) provided a weak test, which produced no evidence in favor of the hypothesis that selection for increased female reproductive rates favors relatively small female body size. Conversely, Martin et al. (1994) suggest that females of highly dimorphic anthropoids show relatively large tooth size and brain size, implying that females of these species cease growth relatively early in ontogeny. We are leery of concluding, as do Martin et al. (1994), that such results indicate that

reduction in female body size is the *primary* cause of variation in body weight dimorphism among primates. On the one hand, in contrast to the supposition of Martin et al. (1994) that dimorphism is achieved primarily through bimaturism, the data of Leigh (1992) clearly demonstrate that dimorphism in a number of taxa is a consequence of accelerated male growth rates. On the other hand, it is difficult to conclude from a static, adult allometric analysis of either tooth size or body size whether males have relatively large brains or teeth, or females have relatively small brains or teeth. Nevertheless, Cochard (1987) concluded that male catarrhines possess relatively small teeth for their body size because males increase body weight late in ontogeny, either through delayed maturation, or an increase in the rate of growth.

Still, it is virtually certain that interspecific variation in weight dimorphism is at least partly a function of variation in female body size. That weight dimorphism exists at all demonstrates that male and female body size are affected by different factors, and it is well known that body size plays an important role in an animal's adaptation to its environment. In fact, recent studies of canine dimorphism (Greenfield, 1992a; Plavcan et al., 1995) demonstrate that a complete understanding of dimorphism can only be achieved by understanding variation in both male and female traits. Elucidation of how changes in female body size effects variation in dimorphism remains a major challenge to understanding the evolution of dimorphism in primates.

Finally, we do not address the role of female choice in the evolution of primate weight dimorphism. Females might prefer to mate with larger males (as in *Saimiri*, Boinski, 1987), resulting in selection for larger male size. In the presence of male-male competition, such female choice should simply re-enforce the effects of male-male competition. It is only where females would consistently prefer to mate with smaller males that selection for increased male body size through male-male competition would be weakened. Although such a mechanism has been suggested for indriid primates

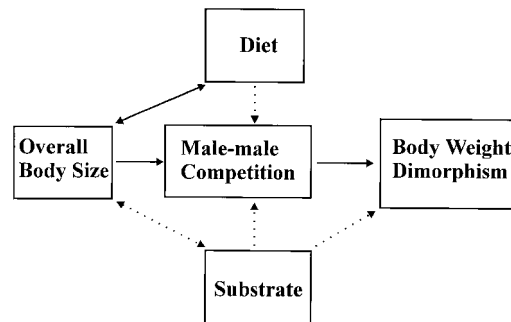


Fig. 6. Path diagram showing hypothesized cause-effect relations among the variables examined in this analysis. Phylogeny is not shown because all variables are affected by phylogeny.

(Richard, 1992), it is unlikely to be common among anthropoids.

CONCLUSIONS

The conclusions of our analysis are summarized in Figure 6, which shows hypothesized cause-effect relations among the variables evaluated here. We find, first, a strong association between male-male competition and body weight dimorphism, corroborating the hypothesis that sexual selection via the mechanism of male-male competition for access to mates plays an important role in the evolution of weight dimorphism in primates. Obviously, male-male competition produces selection specifically affecting male body weight. Our analysis could not address how selection for changes in female body weight affects weight dimorphism.

We suggest that the correlation between female weight and weight dimorphism reflects an interaction between overall body size and male-male competition, and not a fundamental allometric relation (Leutenegger and Cheverud, 1982, 1985). This is consistent with the hypothesis of Mitani et al. (1996) that increasing overall body size is causally associated with increasingly skewed operational sex ratios, as well as that of Kappeler (1990) that there is a body weight threshold, below which selection favors increases in male fighting ability and skill, rather than increased male body weight.

We find only a weak relation between diet and overall weight dimorphism. Still, diet may well be indirectly associated with weight

dimorphism through its correlation with overall body weight, and its relation to female dispersal patterns, which, in turn, influence male mating strategies and male-male competition.

The broad relation between substrate classifications and dimorphism appears to at least partly reflect an interaction between substrate classifications and competition levels. We suggest that correlations between substrate and body weight dimorphism reflect either a correlation between overall size and substrate, or an association between substrate use and patterns of fighting. We cannot rule out a direct constraint of substrate on the expression of size dimorphism.

We do not indicate the relation between phylogeny and dimorphism in Figure 6. This is because we find correlations between phylogeny and all variables in our analysis. We suggest that most taxonomic correlations of weight dimorphism reflect "phylogenetic niche conservatism."

Finally, this analysis was deliberately carried out in a manner similar to that of Plavcan and van Schaik (1992) for canine dimorphism. The results of the two studies strongly parallel one another. This is not surprising given that both canine dimorphism and body weight dimorphism are correlated, and are commonly thought to arise from a common cause: sexual selection through the mechanism of male-male competition for access to females. Still, different patterns are manifest. While there is a strong relation between the potential frequency of male-male competition and canine dimorphism, a similar result is not obtained for body weight dimorphism. Taxonomic correlations of body weight dimorphism are stronger than those of canine dimorphism, especially with regard to colobine primates. Finally, it is notable that, while Plavcan et al. (1995) demonstrate how canine dimorphism is a function of variation in both male and female traits, a similar demonstration for body weight dimorphism has yet to be done (though see Martin et al., 1994), primarily because of the difficulty in evaluating the separate, relative contributions of male and female body weight to body weight dimorphism. Dimorphism in any character can be

a function of changes in either male or female trait values, and a full understanding of weight dimorphism will only follow an analysis of the mechanisms governing the expression of both male and female body size.

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LITERATURE CITED

- Anderson CM (1986) Predation and primate evolution. *Primates* 27:15-39.
- Ayres JM (1981) Observações sobre a ecologia e o comportamento dos cuxiús (*Chiropotes albinasus* e *Chiropotes satanas*, Cebidae, Primates). Manaus, Brazil: Instituto Nacional de Pesquisas da Amazônia (INPA).
- Ayres JM (1986) Uakaris and Amazonian flooded forest. Ph.D. Dissertation, University of Cambridge.
- Blaffer Hrdy S (1977) The Langurs of Abu: Female and Male Strategies of Reproduction. Cambridge: Harvard University Press.
- Boinski S (1987) Mating patterns in squirrel monkeys (*Saimiri oerstedii*). *Behav. Ecol. Sociobiol.* 21:13-21.
- Boinski S (1989) The positional behavior and substrate use of squirrel monkeys: Ecological implications. *J. Hum. Evol.* 18:659-677.
- Booth AH (1957) Observations on the natural history of the olive colobus monkey, *Procolobus verus* (van Beneden). *Proc. Zool. Soc. Lond.* 129:421-430.
- Buchanan-Smith HM (1991) A field study on the red-bellied tamarin, *Saguinus l. labiatus*, in Bolivia. *Int. J. Primatol.* 12:259-276.
- Burtin GJ (1981) The relationship between body and gonadal weights of the dusky leaf monkey. *Int. J. Primatol.* 2:351-368.
- Butynski TM (1988) Guenon birth seasons and correlates with rainfall and food. In A Gautier-Hion, F Bourliere, J Gautier, and J Kingdon (eds.): *A Primate Radiation: Evolutionary Biology of the African Guenons*. Cambridge: Cambridge University Press, pp. 284-322.
- Caldecott JO (1986) Mating patterns, societies and ecogeography of macaques. *Anim. Behav.* 34:208-220.
- Cheverud JM, Dow MM, and Leutenegger W (1985) The quantitative assessment of phylogenetic constraints in comparative analysis: Sexual dimorphism in body weight among primates. *Evolution* 38:1335-1351.
- Clutton-Brock TH (1985) Size, sexual dimorphism, and polygyny in primates. In WL Jungers (ed.): *Size and Scaling in Primate Biology*. New York: Plenum Press, pp. 51-60.
- Clutton-Brock TH and Harvey PH (1978) Mammals, resources and reproductive strategies. *Nature* 273:191-195.
- Clutton-Brock TH, Harvey PH, and Rudder B (1977) Sexual dimorphism, socioeconomic sex ratio and body weight in primates. *Nature* 269:191-195.

- Cochard LR (1987) Postcanine tooth size in female primates. *Am. J. Phys. Anthropol.* 74:47–54.
- Coelho AM (1974) Socio-bioenergetics and sexual dimorphism in primates. *Primates* 15:262–269.
- Coelho AM (1985) Baboon dimorphism: Growth in weight, length and adiposity from birth to 8 years of age. In E Watts (ed.): *Nonhuman Primate Models for Human Growth and Development*. New York: Alan Liss Inc., pp. 125–159.
- Coimbra-Filho AF, and Mittermeier RA (1978) Tree-gouging, exudate-feeding, and the “short-tusked” condition in *Callithrix* and *Cebuella*. In DG Kleiman (ed.): *Biology and Conservation of the Callitrichidae*. Washington, D.C.: Smithsonian Institution Press, pp. 105–116.
- Colyn M (1994) Données pondérales sur les primates Cercopithecidae d’Afrique Centrale (Bassin du Zaïre/Congo). *Mammalia* 58:483–487.
- Coolidge HJ, and Shea BT (1982) External body dimensions of *Pan paniscus* and *Pan troglodytes* chimpanzees. *Primates* 23:245–251.
- Corruccini RS, and McHenry HM (1979) Morphological affinities of *Pan paniscus*. *Science* 204:1341–1343.
- Cowlshaw G, and Dunbar RIM (1991) Dominance and mating success in male primates. *Anim. Behav.* 41:1045–1056.
- Cramer DL, and Zihlman AL (1978) Sexual dimorphism in the pygmy chimpanzee, *Pan paniscus*. In DJ Chivers and KA Joysey (eds.): *Recent Advances in Primatology*. Vol. 3. Evolution. London: Academic Press, pp. 487–490.
- Crile G, and Quiring DP (1940) A record of the body weight and certain organ and gland weights of 3690 animals. *Ohio J. Sci.* 40:219–259.
- Darwin C (1871) *The Descent of Man, and Selection in Relation to Sex*. London: J. Murray.
- Dawson GA, and Dukelow WR (1976) Reproductive characteristics of free-ranging Panamanian tamarins (*Saguinus oedipus geoffroyi*). *J. Med. Primatol.* 5:266–275.
- Dechow PC (1983) Estimation of body weights from craniometric variables in baboons. *Am. J. Phys. Anthropol.* 60:113–123.
- Demment MW (1982) The scaling of ruminoreticulum size with body weight in East African ungulates. *Afr. J. Ecol.* 20:43–47.
- Demment MW (1983) Feeding ecology and the evolution of body size of baboons. *Afr. J. Ecol.* 21:219–233.
- Demment MW, and van Soest PJ (1983) Body size, Digestive Capacity, and Feeding Strategies of Herbivores. Moriston, AR: Winrock International Livestock Research Publications.
- Ely J, and Kurland JA (1989) Spatial autocorrelation, phylogenetic constraints, and the causes of sexual dimorphism in primates. *Int. J. Primatol.* 10:151–171.
- Ely S, Strum S, Muchemi G, and Reid G (1989) Nutrition, body condition, activity patterns, and parasitism of free-ranging troops of olive baboons (*Papio anubis*) in Kenya. *Am. J. Primatol.* 18:209–220.
- Emlen ST, and Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223.
- Fedigan L, and Fedigan LM (1988) *Cercopithecus aethiops*: A review of field studies. In A Gautier-Hion, F Bourliere, J Gautier, and J Kingdon (eds.): *A Primate Radiation: Evolutionary Biology of the African Guenons*. Cambridge: Cambridge University Press, pp. 389–411.
- Fedigan LM, Fedigan L, Chapman C, and Glander KE (1988) Spider monkey home ranges: A comparison of radio telemetry and direct observation. *Am. J. Primatol.* 16:19–29.
- Felsenstein J (1985) Phylogenies and the comparative method. *Am. Nat.* 125:1–15.
- Fleagle JG (1976) Locomotor behavior and skeletal anatomy of sympatric Malaysian leaf-monkeys (*Presbytis obscura* and *Presbytis melalophos*). *Yrbk. Phys. Anthropol.* 20:440–453.
- Fooden J (1963) A revision of the woolly monkeys (genus *Lagothrix*). *J. Mammal.* 44:213–247.
- Fooden J (1964) Stomach contents and gastro-intestinal proportions in wild-shot Guianan monkeys. *Am. J. Phys. Anthropol.* 22:227–232.
- Fooden J (1976) Primates obtained in peninsular Thailand June–July, 1973, with notes on the distribution of the continental southeast leaf-monkeys (*Presbytis*). *Primates* 17:95–118.
- Fooden J (1990) The bear macaque, *Macaca arctoides*: A systematic review. *J. Hum. Evol.* 19:607–686.
- Ford SM (1986) Systematics of the New World monkeys. In DR Swindler and J Erwin (eds.): *Comparative Primate Biology, Vol. 1: Systematics, Evolution, and Anatomy*. New York: Alan R. Liss, pp. 73–135.
- Ford SM (1994) Evolution of sexual dimorphism in body weight in platyrrhines. *Am. J. Primatol.* 34:221–244.
- Ford SM, and Davis LC (1992) Systematics and body size: Implications for feeding adaptations in New World monkeys. *Am. J. Phys. Anthropol.* 88:415–468.
- Garber PA, and Teaford MF (1986) Body weights in mixed species troops of *Saguinus mystax mystax* and *Saguinus fuscicollis nigrifrons* in Amazonian Peru. *Am. J. Phys. Anthropol.* 71:331–336.
- Garber PA, Encarnacion F, Moya L, and Pruett JD (1993) Demographic and reproductive patterns in mustached tamarin monkeys (*Saguinus mystax*): Implications for reconstructing platyrrhine mating systems. *Am. J. Primatol.* 29:235–254.
- Gaulin SJC, and Sailer LD (1984) Sexual dimorphism in weight among the primates: The relative impact of allometry and sexual selection. *Int. J. Primatol.* 5:515–535.
- Gautier-Hion A (1975) Dimorphisme sexuel et organisation sociale chez les cercopithécins forestiers africains. *Mammalia* 39:365–374.
- Gautier-Hion A, and Gautier J (1985) Sexual dimorphism, social units and ecology among sympatric forest guenons. In J Guesquiere, RD Martin, and F Newcombe (eds.): *Human Sexual Dimorphism*. London: Taylor and Francis, pp. 61–77.
- Geist V (1965) The evolution of horn-like organs. *Behavior* 27:174–213.
- Godfrey LR, Lyon SK, and Sutherland MR (1993) Sexual dimorphism in large-bodied primates: The case of the subfossil lemurs. *Am. J. Phys. Anthropol.* 90:315–334.
- Green KM (1981) Preliminary observations on the ecology and behavior of the capped langur, *Presbytis pileatus*, in the Modhupur Forest of Bangladesh. *Int. J. Primatol.* 2:131–151.
- Greenfield LO (1992a) Origin of the human canine: A new solution to an old enigma. *Yrbk. Phys. Anthropol.* 35:153–185.
- Greenfield LO (1992b) Relative canine size, behavior, and diet in male ceboids. *J. Hum. Evol.* 23:469–480.
- Haddow AJ (1952) Field and laboratory studies on an African monkey, *Cercopithecus ascanius schmidtii* Matschie. *Proc. Zool. Soc. Lond. B* 122:297–398.
- Harvey PH, and Pagel M (1991) *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.
- Harvey PH, Martin RD, and Clutton-Brock TH (1987) Life histories in comparative perspective. In BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham, and TT Struhsaker (eds.): *Primate Societies*. Chicago: University of Chicago Press, pp. 181–196.

- Hershkovitz P (1985) A preliminary taxonomic review of the South American bearded saki monkeys genus *Chiropotes* (Cebidae, Platyrrhini), with the description of a new subspecies. *Fieldiana* n. s. 27:1–46.
- Hershkovitz P (1990) Titis, New World monkeys of the genus *Callicebus* (Cebidae, Platyrrhini): A preliminary taxonomic review. *Fieldiana* (Zoology) n. s. 55:1–109.
- Hill WCO (1957) *Primates: Comparative Anatomy and Taxonomy*. Vol. III. (Pithecoidea) Platyrrhini. Edinburgh: University Press.
- Hill WCO (1960) *Primates: Comparative Anatomy and Taxonomy*. Vol. IV. (Cebidae) Part A. Edinburgh: University Press.
- Hill WCO (1966) *Primates: Comparative Anatomy and Taxonomy*. Catarrhini, Cercopithecoidea, Cercopithecinae. Vol. 6. Edinburgh: University Press.
- Hill WCO (1974) *Primates: Comparative Anatomy and Taxonomy*. Cynopithecinae: *Cercocebus*, *Macaca*, *Cynopithecus*. Vol. 7. Edinburgh: University Press.
- Horrocks JA (1986) Life-history characteristics of a wild population of vervets (*Cercopithecus aethiops sabaeus*) in Barbados, West Indies. *Int. J. Primatol.* 7:31–47.
- Hrdlicka A (1925) Weight of the brain and of the internal organs in American monkeys. *Am. J. Phys. Anthropol.* 8:201–211.
- Hurov JR (1987) Terrestrial locomotion and back anatomy in vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*). *Am. J. Primatol.* 13:297–311.
- Husson AM (1978) *The Mammals of Suriname*. Leiden: E.J. Brill.
- Jolly CJ (1993) Species, subspecies, and baboon systematics. In WH Kimbel and LB Martin (eds.): *Species, Species Concepts, and Primate Evolution*. New York: Plenum Press, pp. 67–107.
- Jungers WL (1985) Body size and scaling of limb proportions in primates. In WL Jungers (ed.): *Size and Scaling in Primate Biology*. New York: Plenum Press, pp. 345–381.
- Jungers WL, and Sussman RL (1984) Body size and skeletal allometry in African apes. In RL Sussman (ed.): *The Pygmy Chimpanzee. Evolutionary Biology and Behavior*. New York: Plenum Press, pp. 131–177.
- Kappeler PM (1990) The evolution of sexual size dimorphism in prosimian primates. *Am. J. Primatol.* 21:201–214.
- Kappeler, PM (1991) Patterns of sexual dimorphism in body weight among prosimian primates. *Folia Primatol.* 57:132–146.
- Kay RF (1990) The phyletic relationships of extant and fossil Pitheciinae (Platyrrhini, Anthropoidea). *J. Hum. Evol.* 19:175–208.
- Kay RF, Plavcan JM, Glander KE, and Wright PC (1988) Sexual selection and canine dimorphism in New World monkeys. *Am. J. Phys. Anthropol.* 77:385–397.
- Kunkun JG (1986) Ecology and behavior of *Presbytis thomasi* in northern Sumatra. *Primates* 27:151–172.
- Lande R (1980) Sexual dimorphism, sexual selection and adaptation in polygenic characteristics. *Evolution* 34:292–307.
- Leigh SR (1992) Patterns of variation in the ontogeny of primate body size dimorphism. *J. Hum. Evol.* 23:27–50.
- Leigh SR (1994) Relations between captive and noncaptive weights in anthropoid primates. *Zool. Biol.* 13:21–43.
- Leigh SR (1995) Socioecology and the ontogeny of sexual size dimorphism in anthropoid primates. *Am. J. Phys. Anthropol.* 97:339–356.
- Leigh SR, and Shea BT (1994) Ontogeny and the evolution of body size dimorphism in apes. *Am. J. Primatol.* 36:37–60.
- Lemos de Sa RM, and Glander KE (1993) Morphometrics of the woolly spider monkey, or miriqui (*Brachyteles arachnoides*, E. Geoffroy 1806). *Am. J. Primatol.* 29:145–153.
- Leutenegger W, and Cheverud JM (1982) Correlates of sexual dimorphism in primates: Ecological and size variables. *Int. J. Primatol.* 3:387–402.
- Leutenegger W, and Cheverud JM (1985) Sexual dimorphism in primates: The effects of size. In WL Jungers (ed.): *Size and Scaling in Primate Biology*. New York: Plenum Press, pp. 33–50.
- Leutenegger W, and Kelly JT (1977) Relationship of sexual dimorphism in canine size and body size to social, behavioral, and ecological correlates in anthropoid primates. *Primates* 18:117–136.
- Lucas PW, Corlett RT, and Luke DA (1986) Sexual dimorphism in tooth size in anthropoids. *Hum. Evol.* 1:23–39.
- Lyon MW, Jr. (1908a) Mammals collected by Dr. W.L. Abbott on Borneo and some of the small adjacent islands. *Proc. U.S. Natl. Mus.* 40:53–159.
- Lyon MW, Jr. (1908b) Mammals collected in western Borneo by Dr. W.L. Abbott. *Proc. U.S. Natl. Mus.* 33:547–571.
- Maddison WP, Donoghue MJ, and Maddison DR (1984) Outgroup analysis and parsimony. *Syst. Zool.* 33:83–103.
- Markham R, and Groves CP (1990) Brief Communication: Weights of wild Orang Utans. *Am. J. Phys. Anthropol.* 81:1–3.
- Martin RD, Willner LA, and Dettling A (1994) The evolution of sexual size dimorphism in primates. In RV Short and E Balaban (eds.): *The Differences Between the Sexes*. Cambridge: Cambridge University Press, pp. 159–200.
- McHenry HM (1991) Sexual dimorphism in *Australopithecus afarensis*. *J. Hum. Evol.* 20:21–32.
- Miller GS, Jr. (1903) Seventy new malayan mammals. *Smithson. Misc. Coll.* 45:1–73.
- Milton K (1982) Dietary quality and demographic regulation in a howler monkey population. In EG Leigh, Jr, ES Rand, and DM Windsor (eds): *The Ecology of a Tropical Rain Forest: Seasonal Rhythms and Long-Term Changes*. Washington, DC: Smithsonian Institution Press, pp. 273–289.
- Milton K (1984) The role of food-processing factors in primate food choice. In PS Rodman and JGS Cant (eds.): *Adaptations for Foraging in Nonhuman Primates*. New York: Columbia University Press, pp. 249–279.
- Milton K (1985) Multimale mating and the absence of canine tooth dimorphism in woolly spider monkeys (*Brachyteles arachnoides*). *Am. J. Phys. Anthropol.* 68:519–523.
- Mitani J, Gros-Louis J, and Richards, AF (1996) Sexual dimorphism, the operational sex ratio, and the intensity of male competition in polygynous primates. *Am. Nat.* 147:966–980.
- Mittermeier RA (1977) *Distribution, Synecology, and Conservation of Suriname Monkeys*. Ph.D. Dissertation, Harvard University.
- Morbeck ME, and Zihlman AL (1989) Body size and proportions in chimpanzees, with special reference to *Pan troglodytes schweinfurthii* from Gombe National Park, Tanzania. *Primates* 30:369–382.
- Murie A (1935) *Mammals from Guatemala and British Honduras*. Univ. Mich. Mus. Zool. Misc. Publ. 26:5–33.
- Napier PH (1981) *Catalogue of Primates in the British Museum (Natural History)*, Part II: Family Cercopi-

- thecidae, Subfamily Cercopithecinae. London: British Museum (Natural History).
- Napier PH (1985) Catalogue of Primates in the British Museum (Natural History), Part III: Family Cercopithecidae, Subfamily Colobinae. London: British Museum (Natural History).
- Neyman PF (1978) Aspects of the ecology and social organization of free-ranging cotton-top tamarins (*Saguinus oedipus*) and the conservation status of the species. In DG Kleiman (ed.): *The Biology and Conservation of the Callitrichidae*. Washington, D.C.: Smithsonian Institution Press, pp. 39–71.
- Oates JF (1988) The diet of the olive colobus monkey, *Procolobus verus*, in Sierra Leone. *Int. J. Primatol.* 9:457–478.
- Oates JF, Davies AG, and Delson E (1995) The diversity of living colobines. In AG Davies and JF Oates (eds.): *Colobine Monkeys: Their Ecology, Behaviour and Evolution*. Cambridge: Cambridge University Press, pp. 45–73.
- Oboussier H, and von Maydell GA (1959) Zur Kenntnis des indischen Goldlangurs, Ergebnisse der Deutschen Indien-Expedition 1955–1957. *Leitung, GA Frhr. V Maydell. Z. Okol. Tiere (Berlin)* 58:102–114.
- Oliveira JMS, Bonvincino C, Ayres JM, and Fleagle JG (1985) Preliminary notes on the ecology and behavior of the Guianan Saki (*Pithecia pithecia*, Linnaeus 1766; Cebidae, Primate). *Acta Amazonica* 15:249–263.
- Pagel M (1992) A method for the analysis of comparative data. *J. Theor. Biol.* 156:431–442.
- Palombit RA (1993) Lethal territorial aggression in a white-handed gibbon. *Am. J. Primatol.* 31:311–318.
- Peres CA (1993) Notes on the primates of the Jurua river, western Brazilian Amazonia. *Folia Primatol.* 61:97–103.
- Peres CA (1994) Which are the largest New World monkeys? *J. Hum. Evol.* 26:245–249.
- Phillips-Conroy JE, and Jolly CJ (1981) Sexual dimorphism in two subspecies of Ethiopian baboons (*Papio hamadryas*) and their hybrids. *Am. J. Phys. Anthropol.* 56:115–129.
- Pickford, M (1986) On the origins of body size dimorphism in primates. In M Pickford and B Chiarelli (eds.): *Sexual Dimorphism in Living and Fossil Primates*. Firenze: Il Sedicesimo, pp. 77–91.
- Plavcan JM (1990) Sexual Dimorphism in the Dentition of Extant Anthropoid Primates. Ph.D. Dissertation, University Microfilms, Ann Arbor, Michigan.
- Plavcan JM (1993) Canine size and shape in male anthropoid primates. *Am. J. Phys. Anthropol.* 92:201–216.
- Plavcan JM (1994) Comparison of four simple methods for estimating sexual dimorphism in fossils. *Am. J. Phys. Anthropol.* 94:465–476.
- Plavcan JM, and van Schaik CP (1992) Intrasexual competition and canine dimorphism in anthropoid primates. *Am. J. Phys. Anthropol.* 87:461–477.
- Plavcan JM, and van Schaik CP (1994) Canine Dimorphism. *Evol. Anthropol.* 2:208–214.
- Plavcan JM, van Schaik CP, and Kappeler PM (1995) Competition, coalitions and canine size in primates. *J. Hum. Evol.* 28:245–276.
- Pocock R (1939) *The Fauna of British India, Including Ceylon and Burma: Mammalia. I. Primates and Carnivora (in Part), Families Felidae and Viverridae*, 2nd ed. London: Taylor and Francis.
- Pusey AE (1978) The physical and social development of wild adolescent chimpanzees (*Pan troglodytes schweinfurthii*). Ph.D. Dissertation, Stanford University.
- Raemaekers JJ and Raemaekers PM (1985) Field playback of loud calls to gibbons (*Hylobates lar*): Territorial, sex-specific and species specific responses. *Anim. Behav.* 33:481–493.
- Rahm U (1967) Observations during chimpanzee captures in the Congo. In Stark D, Schneider R, and Kuhn HJ (eds.): *Progress in Primatology*. Stuttgart: Fischer, pp. 195–207.
- Ralls K (1976) Mammals in which females are larger than males. *Q. Rev. Biol.* 51:245–276.
- Ranta E, Anssi L, and Elmberg J (1994) Reinventing the wheel: Analyses of sexual dimorphism in body size. *Oikos* 70:313–321.
- Richard AF (1992) Aggressive competition between males, female-controlled polygyny and sexual monomorphism in a Malagasy primate, *Propithecus verreauxi*. *J. Hum. Evol.* 22:395–406.
- Robinson JG, and Ramirez CJ (1982) Conservation biology of Neotropical primates. In MA Mares and HH Genoways (eds.): *Mammalian Biology in South America. Special Publication Series Pymatuning Laboratory of Ecology University of Pittsburgh*, 6:329–344.
- Rodman PS (1984) Foraging and social systems of orangutans and chimpanzees. In PS Rodman and JGH Cant (eds.): *Adaptations for Foraging in Nonhuman Primates*. New York: Columbia University Press, pp. 134–150.
- Roonwall ML, and Mohnot SM (1977) *Primates of South Asia: Ecology, Sociobiology, and Behavior*. Cambridge: Harvard University Press.
- Rosenberger AL (1979) Phylogeny, evolution and classification of New World Monkeys (Platyrrhini, Primates). Ph. D. Dissertation, City University of New York.
- Rosenberger AL (1981) Systematics: The higher taxa. In AF Coimbra-Filho and RA Mittermeir (eds.): *Ecology and Behavior of Neotropical Primates*, Vol. 1. Rio de Janeiro: Academia Brasileira de Ciências, pp. 9–27.
- Rosenberger AL, and Coimbra-Filho AF (1984) Morphology, taxonomic status and affinities of the lion tamarins (*Leontopithecus*) (Callitrichinae, Cebidae). *Folia Primatol.* 42:149–179.
- Rosenberger AL, and Strier KB (1989) Adaptive radiation of the ateline primates. *J. Hum. Evol.* 18:717–750.
- Rothenthal E (1976) Überprüfung der Gewichtsangaben adulterer Primaten. *Sem. Arbeit. Univ. Zürich*.
- Rowell TE, and Chism J (1986) Sexual dimorphism and mating systems: Jumping to conclusions. In M Pickford and B Chiarelli (eds.): *Sexual Dimorphism in Living and Fossil Primates*. Firenze: Il Sedicesimo, pp. 107–111.
- Rudran, R (1973) Adult male replacement in one-male troops of purple-faced langurs (*Presbytis senex senex*) and its effect of population structure. *Folia Primatol.* 19:166–192.
- Rushi A (1964) *Macacos do estado do Espirito Santo*. Bol. Mus. Biol. Prof. Mello Leitao, 23A:1–23.
- Sanderson IT (1949) A brief review of the mammals of Suriname (Dutch Guiana), based on a collection made in 1938. *Proc. Zool. Soc. Lond.* 119:755–789.
- Schultz AH (1940) The size of the orbit and of the eye in primates. *Am. J. Phys. Anthropol.* 26:389–408.
- Schultz AH (1941) The relative size of the cranial capacity in primates. *Am. J. Phys. Anthropol.* 28:273–287.
- Schultz AH (1944) Age changes and variability in gibbons. *Am. J. Phys. Anthropol.* 2:1–129.
- Schultz AH (1973) The skeleton of the Hylobatidae and other observations on their morphology. *Gibbon Siamang* 2:1–54.
- Shea BT (1986) Ontogenetic approaches to sexual dimorphism in anthropoids. *Hum. Evol.* 1:97–110.
- Smith RJ (1981) Interspecific scaling of maxillary canine size and shape in female primates: Relationships to social structure and diet. *J. Hum. Evol.* 10:165–173.

- Smith RJ (1996) Biology and body size in human evolution: Statistical inference misapplied. *Curr. Anthropol.* 37:2–36.
- Snowden PT, and Soini P (1988) The tamarins, genus *Saguinus*. In RA Mittermeier, AB Rylands, AF Coimbra-Filho, and GAB da Fonseca (eds.): *Ecology and Behavior of Neotropical Primates*, Vol. 2. Washington, D.C.: World Wildlife Fund, pp. 223–298.
- Soini P (1988) The pygmy marmoset, genus *Cebuella*. In RA Mittermeier, AB Rylands, AF Coimbra-Filho, and GAB da Fonseca (eds.): *Ecology and Behavior of Neotropical Primates*, Vol. 2. Washington, D.C.: World Wildlife Fund, pp. 79–129.
- Sokal RR, and Rohlf FJ (1995) *Biometry*. Third Edition. New York: WH Freeman and Company.
- Stewart KJ, and Harcourt AH (1987) Gorillas: Variation in female relationships. In BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham, and TT Struhsaker (eds.): *Primate Societies*. Chicago: University of Chicago Press, pp. 155–164.
- Stoltz L (1977) Population dynamics of baboons, *P. ursinus*, in the Transvaal. Ph.D. Dissertation, University of Pretoria.
- Strasser E (1992) Hindlimb proportions, allometry, and biomechanics in Old World monkeys (Primates, Cercopithecidae). *Am. J. Phys. Anthropol.* 87:187–213.
- Struhsaker (1975) *The Red Colobus Monkey*. Chicago: University of Chicago Press.
- Struhsaker TT, and Leland L (1979) Sociocology of five sympatric monkey species in the Kibak Forest, Uganda. In J. Rosenblatt and RA Hinde (eds.): *Advances in the Study of Behavior*, Vol. 9. New York: Academic Press, pp. 158–228.
- Strum SC (1991) Weight and age in wild olive baboons. *Am. J. Primatol.* 25:219–237.
- Tilson RL, and Tenaza RR (1976) Monogamy and duetting in an Old World monkey. *Nature* 263:320–321.
- Turner TR, Anapol F, and Jolly CF (1994) Body weights of adult vervet monkeys (*Cercopithecus aethiops*) at four sites in Kenya. *Folia Primatol.* 63:177–179.
- Uehara S, and Nishida T (1987) Body weights of wild chimpanzees (*Pan troglodytes schweinfurthii*) of the Mahale Mountains National Park, Tanzania. *Am. J. Phys. Anthropol.* 72:315–321.
- van Hippiel FA (1996) Interactions between overlapping multimale groups of black and white colobus monkeys (*Colobus guereza*) in the Kakamega Forest, Kenya. *Am. J. Primatol.* 38:193–209.
- van Roosmalen MGM (1985) Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (*Ateles paniscus paniscus* Linnaeus 1758) in Surinam. *Acta Amazonica* 15:3–230.
- Wilkinson L (1990) SYSTAT: The System for Statistics. Evanston: SYSTAT, Inc.
- Wrangham RW, and Smuts BB (1980) Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. *J. Reprod. Fertil. (Suppl.)* 28:13–31.
- Yoneda M (1981) Ecological studies of *Saguinus fuscicollis* and *Saguinus labiatus* with reference to habitat segregation and height preference. *Kyoto Univ. Overseas Res. Rep. New World Monkeys* 2:43–50.

APPENDIX A. Male and female body weights (in kg), competition levels (Com), substrate classifications (Sub), and dietary classifications used in this analysis (body weights used in the analysis are listed first for each species)

Species	Male weight	Female weight	Dim	Com	Sub ¹	Diet ²	Reference
<i>Cercocebus albigena</i>	8.98 (5)	6.40 (6)	1.40	4	A	Frug	Gautier-Hion (1975)
	7.65 (4)	6.50 (6)	1.18				Colyn (1994) <i>C. a. johnstoni</i>
	7.34 (4)	4.92 (4)	1.49				Colyn (1994) <i>C. a. albigena</i>
	7.31 (4)	5.67 (3)	1.29				Napier (1981)
	6.35 (4)	4.92 (2)	1.29				Strasser (1992)
<i>Cercocebus galeritus</i>	10.00	7.00	1.43	4	A/T	Frug	Butynski (1988)
	10.18 (3)	5.47 (3)	1.86				Gautier-Hion (1975)
	9.50 (2)	5.66 (2)	1.68				Colyn (1994) <i>C. g. agilis</i>
<i>Cercocebus torquatus</i>	11.41 (4)	6.33 (3)	1.80	4	A/T	Frug	Strasser (1992)
	10.20	5.50	1.85				Harvey et al. (1987)
<i>Cercopithecus aethiops</i> ³	4.58 (17)	3.26 (15)	1.40	4	A/T	Frug	Napier (1981)
	5.30 (61)	3.30 (71)	1.61				Horrocks (1986)
	5.37 (10)	3.60 (7)	1.49				Jungers (1985)
	3.30 (2)	2.90 (1)	1.14				Hill (1966)
	4.13 (26)	2.57 (36)	1.61				Turner et al. (1994) (Sam-buru, Kenya)
	4.24 (4)	2.75 (10)	1.54				Turner et al. (1994) (Mosiro, Kenya)
	4.43 (12)	3.44 (31)	1.29				Turner et al. (1994) (Nai-vasha, Kenya)
	4.33 (18)	3.15 (15)	1.37				Turner et al. (1994) (Kimana, Kenya)
	5.10	3.50	1.46				Butynski (1988)
	7.00	5.60	1.25				Fedigan and Fedigan (1988)
<i>Cercopithecus ascanius</i>	4.75	3.56	1.33	3	A	Frug	Harvey et al. (1987)
	3.71 (32)	2.96 (187)	1.25				Colyn (1994) <i>C. a. katangae</i>
	3.69 (37)	2.78 (55)	1.33				Colyn (1994) <i>C. a. schmidtii</i> (Kisangani, Zaire)
	4.21 (6)	3.30 (2)	1.28				Napier (1981)
	4.20	2.90	1.45				Butynski (1988)
	9.20	6.40	1.44				Haddow (1952) cited in Gaulin and Sailer (1984)
	4.09 (8)	2.88 (10)	1.42				Gautier-Hion (1975)
	8.50	4.70	1.81				Harvey et al. (1987)
<i>Cercopithecus lhoesti</i>	5.97 (19)	3.45 (50)	1.73	3	A/T	Frug	Colyn (1994)
<i>Cercopithecus mitis</i>	5.85 (41)	3.93 (94)	1.49	3	A	Frug	Colyn (1994) <i>C. m. stuhlmanni</i>
	7.35 (12)	4.23 (14)	1.74				Napier (1985)
	4.55 (1)	2.90 (2)	1.57				Crile and Quiring (1940)
	8.63 (3)	4.32 (5)	2.00				Strasser (1992)
	6.90	4.20	1.64				Butynski (1988)
<i>Cercopithecus mona</i>	7.60	4.40	1.73	3	A/T	Frug	Harvey et al. (1987)
	4.40	2.50	1.76				Harvey et al. (1987)
	5.00	4.00	1.25				Hill (1966) cited in Strasser (1992)
	6.32 (8)	3.96 (8)	1.60				Jungers (1985)
<i>Cercopithecus neglectus</i>	8.05 (2)	4.46 (2)	1.80	3	A/T	Frug	Napier (1981)
<i>Cercopithecus nictitans</i>	7.00 (4)	3.96 (4)	1.77	3	A	Frug	Gautier-Hion (1975)
	6.73 (17)	4.28 (21)	1.57				Colyn (1994) <i>C. n. nictitans</i>
	6.60 (16)	4.22 (9)	1.56				Gautier-Hion (1975)
<i>Cercopithecus pogonias</i>	4.50 (4)	3.02 (6)	1.49	3	A	Frug	Gautier-Hion (1975)
	3.30 (1)	2.70 (4)	1.22				Colyn (1994) <i>C. p. grayi</i>
	4.60 (1)	3.00 (1)	1.53				Strasser (1992)
<i>Colobus angolensis</i> ⁴	9.62 (8)	7.77 (5)	1.24	4	A	Fol	Colyn (1994) <i>C. a. angolensis</i>
	9.68 (2)	7.40 (5)	1.31				Napier (1985)
	9.80 (4)	7.40 (6)	1.32				Oates et al. (1995)
	10.70	9.00	1.19				Harvey et al. (1987)

APPENDIX A. (continued)

Species	Male weight	Female weight	Dim	Com	Sub ¹	Diet ²	Reference
<i>Colobus badius</i> ⁵	9.35 (7)	6.77 (7)	1.38	4	A	Fol	Napier (1985)
	7.65 (2)	5.68 (10)	1.35				Colyn (1994) <i>C. b. langi</i>
	9.20 (1)	7.47 (6)	1.23				Colyn (1994) <i>C. b. parmentierorum</i>
	12.50 (1)	8.25 (2)	1.52				Colyn (1994) <i>C. b. oustaleti</i>
	10.50 (1)	5.75 (1)	1.83				Struhsaker (1975)
	8.30 (9)	8.20 (16)	1.01				Oates et al. (1995) (<i>C. b. badius</i>)
	9.23 (3)	7.15 (1)	1.29				WS McGraw (personal communication)
	10.50	7.00	1.50				Struhsaker and Leland (1979) cited in Oates et al. (1995) (<i>C. b. tephrosceles</i>)
<i>Colobus guereza</i> ⁶	9.33 (8)	7.83 (12)	1.19	3	A	Fol	Napier (1985)
	10.10 (10)	8.04 (10)	1.26				Jungers (1985)
	13.50 (3)	9.20 (4)	1.47				Oates et al. (1995) (<i>C. g. guereza</i>)
	10.10 (4)	7.90 (7)	1.28				Oates et al. (1995) (<i>C. g. matschiei</i>)
	11.80	9.25	1.28				Harvey et al. (1987)
<i>Colobus polykomos</i>	10.70	9.00	1.19	4	A	Fol	Gaulin and Sailer (1984)
	9.90 (5)	8.30 (10)	1.19				Oates et al. (1995)
	8.42 (5)	7.13 (6)	1.18				Napier (1985)
	8.00 (1)	9.70 (1)	0.82				Strasser (1992)
	10.40	8.40	1.24				Harvey et al. (1987)
<i>Colobus satanas</i>	12.00	9.50	1.26	4	A	Fol	Harvey et al. (1987)
	10.00	9.00	1.11				Clutton-Brock et al. (1977)
<i>Colobus verus</i>	4.60 (22)	4.10 (17)	1.12	4	A	Fol	Oates (1988)
	4.70 (20)	4.20 (14)	1.12				Oates et al. (1995)
	4.00 (1)	3.50 (2)	1.14				Napier (1985)
	4.39 (9)	3.83 (5)	1.15				Strasser (1992)
	3.80 (7)	3.60 (5)	1.06				Booth (1957) cited in Strasser (1992)
	5.12 (1)	5.50 (1)	0.93				WS McGraw (personal communication)
<i>Erythrocebus patas</i>	11.10 (3)	5.90 (5)	1.88	3	S	Fr/Ins	Jungers (1985)
	8.18 (3)	4.40 (1)	1.86				Hurov (1987) cited in Strasser (1992)
	10.00	5.60	1.78				Harvey et al. (1987)
<i>Gorilla gorilla</i>	12.00	6.00	2.00	3	A/T	Fol	Butynski (1988)
	159.20 (7)	97.70 (8)	1.63				Jungers (1985)
	160.00	93.00	1.72				Harvey et al. (1987)
	160.00	95.00	1.68				Stewart and Harcourt (1987)
<i>Hylobates concolor</i>	5.60 (10)	5.80 (11)	0.96	1	A	Frug	Schultz (1973)
<i>Hylobates hoolock</i>	6.26 (4)	5.78 (2)	1.08	1	A	Frug	Lyon (1908b)
	6.90 (5)	6.50 (2)	1.06				Schultz (1973)
<i>Hylobates klossi</i>	6.90	6.10	1.13	1	A	Fr/Ins	Gaulin and Sailer (1984)
	5.70 (2)	5.90 (4)	0.97				Schultz (1973)
	5.66 (2)	5.89 (4)	0.96				Miller (1903)
<i>Hylobates lar</i> ⁷	5.71 (43)	5.30 (37)	1.08	1	A	Frug	Schultz (1944)
<i>Hylobates syndactylus</i>	10.85 (10)	10.60 (9)	1.02	1	A	Fol	Schultz (1973)
	12.74 (1)	12.25 (2)	1.04				Hrdlicka (1925)
	12.24 (2)	10.60 (2)	1.15				Miller (1903)
	11.10	10.30	1.08				Gaulin and Sailer (1984)
<i>Macaca arctoides</i>	12.20 (6)	8.40 (3)	1.45	4	A/T	Frug	Fooden (1990)
<i>Macaca fascicularis</i> ⁸	4.54 (8)	3.12 (15)	1.46	4	A/T	Frug	Field notes, MCZH
	6.20 (3)	4.54 (3)	1.36				Napier (1981)
	4.93 (6)	3.13 (6)	1.58				Jungers (1985)
	5.32 (5)	3.90 (1)	1.36				Lyon (1908a)
	4.16 (3)	3.18 (6)	1.31				Strasser (1992)
	5.90	4.10	1.44				Harvey et al. (1987)
	11.70	9.10	1.28				Harvey et al. (1987)
<i>Macaca fuscata</i>	11.00	9.20	1.20	4	A/T	—	Gaulin and Sailer (1984)

APPENDIX A. (continued)

Species	Male weight	Female weight	Dim	Com	Sub ¹	Diet ²	Reference
<i>Macaca mulatta</i> ⁹	6.80 (4) 7.71 (8)	5.18 (6) 5.37 (9)	1.31 1.44	4	A/T	Frug	Napier (1981) (<i>M. m. mulatta</i>) Napier (1981) (all specimens) Schultz (1940) Schultz (1941) Harvey et al. (1987)
<i>Macaca nemestrina</i> ¹⁰	6.20 10.21 (6) 9.75 (2) 9.99 (1) 9.99 (1) 10.40 13.00	3.00 6.35 (6) 4.65 (1) 5.98 (3) 5.83 (3) 7.80 7.00	2.07 1.61 2.10 1.67 1.71 1.33 1.86	4	A/T	Frug	Jungers (1985) Napier (1981) Schultz (1940) Strasser (1992) Harvey et al. (1987) Caldecott (1986)
<i>Macaca nigra</i>	7.99 (3) 10.40	4.69 (3) 6.60	1.70 1.58	4	A/T	Frug	Hill (1966, 1974) cited in Strasser (1992) Harvey et al. (1987) Harvey et al. (1987)
<i>Macaca silenus</i>	6.80	5.00	1.36	4	A/T	—	Harvey et al. (1987)
<i>Macaca sinica</i>	6.50 5.70	3.40 3.60	1.91 1.58	4	A/T	Frug	Harvey et al. (1987) Gaulin and Sailer (1984)
<i>Mandrillus leucophaeus</i>	17.00	10.00	1.70	4	A/T	Frug	Harvey et al. (1987)
<i>Miopithecus talapoin</i>	1.38 (7)	1.12 (9)	1.23	4	A	Fr/Ins	Gautier-Hion (1975)
<i>Nasalis larvatus</i> ¹¹	21.20 (13) 20.35 (9) 20.35 (9) 20.37 (6) 20.63 (6) 19.00 (1) 18.43 (8)	10.00 (14) 9.87 (14) 10.00 (14) 9.82 (6) 10.20 (2) 9.05 (2) 8.36 (3)	2.12 2.06 2.04 2.07 2.02 2.10 2.20	4	A	Fol	Oates et al. (1995) Schultz (1941) Schultz (1940) Jungers (1985) Lyon (1908b) Lyon (1908a) Strasser (1992)
<i>Pan paniscus</i> ¹²	45.00 (10) 54.50 (2) 38.30 (8) 39.80 (8) 47.80 (5) 45.50 (4)	33.20 (10) 37.00 (1) 32.20 (5) 31.20 (8) 33.10 (7) 33.40 (6)	1.36 1.47 1.19 1.28 1.44 1.36	2	A/T	Frug	Jungers (1985) Coolidge and Shea (1982) Corruccini and McHenry (1979) Cramer and Zihlman (1978) McHenry (1991) Morbeck and Zihlman (1989)
<i>Pan troglodytes</i> ¹³	43.00 (15) 54.20 (6) 56.69 (1) 60.00 (20) 42.30 (11) 39.50 (9) 42.80 (3) 42.00 (6) 39.50 41.60 49.00	33.2 (19) 39.7 (9) 43.99 (1) 47.40 (20) 30.00 (7) 29.80 (6) 34.30 (9) 35.20 (8) 29.80 31.10 41.00	1.30 1.36 1.29 1.26 1.41 1.32 1.25 1.19 1.33 1.34 1.20	2	A/T	Frug	Jungers and Sussman (1984) (<i>P. t. schweinfurthi</i>) McHenry (1991) Crile and Quiring (1940) Jungers (1985) (<i>P. t. troglodytes</i>) Pusey (1978) cited in Uehara and Nishida (1987) (<i>P. t. schweinfurthi</i>) Wrangham and Smuts (1980) cited in Uehara and Nishida (1987) (<i>P. t. schweinfurthi</i>) Rahm (1967) cited in Uehara and Nishida (1987) (<i>P. t. schweinfurthi</i>) Uehara and Nishida (1987) (<i>P. t. schweinfurthi</i>) Rodman (1984) Harvey et al. (1987) Gaulin and Sailer (1984)

APPENDIX A. (continued)

Species	Male weight	Female weight	Dim	Com	Sub ¹	Diet ²	Reference
<i>Papio anubis</i> ¹⁴	25.10 (37)	14.10 (16)	1.78	4	S	Frug	Dechow (1983)
	28.41 (4)	14.74 (2)	1.93				Napier (1981)
	22.50 (28)	13.70 (20)	1.64				Demment (1983)
	24.00	14.70	1.63				Strum (1991)
	27.40	15.60	1.76				Strum (1991) ("crop raiders")
	23.64	15.60	1.52				Ely et al. (1989) cited in Strum (1991)
	29.20	16.85	1.73				Coelho (1985) cited in Strum (1991)
	25.40	14.50	1.76				Stoltz (1977) cited in Strum (1991)
	21.00	12.00	1.75				Harvey et al. (1987)
	26.00	13.00	2.00				Gaulin and Sailer (1984)
<i>Papio cynocephalus</i> ¹⁵	17.24 (1)	9.75 (1)	1.77	4	S	Frug	Napier (1981) (Kinda baboon)
	24.89 (3)	13.61 (1)	1.83				Napier (1981) (other <i>P. cynocephalus</i>)
	22.80 (4)	12.35 (6)	1.85				Jungers (1985)
	22.93 (5)	12.11 (6)	1.89				Strasser (1992)
	22.80 (20)	15.90 (1)	1.43				Dechow (1983)
	20.00	15.00	1.33				Harvey et al. (1987)
	19.58 (10)	9.98 (5)	1.96				Strasser (1992)
	21.30 (13)	12.00 (2)	1.78				Dechow (1983)
	21.50	9.40	2.29				Harvey et al. (1987)
	27.45 (3)	14.52 (3)	1.89				Strasser (1992)
<i>Papio hamadryas</i>	21.30 (13)	12.00 (2)	1.78	4	S	Fr/Fol	Dechow (1983)
<i>Papio ursinus</i>	21.50	9.40	2.29				Harvey et al. (1987)
<i>Papio ursinus</i>	27.45 (3)	14.52 (3)	1.89	4	S	Fr/Fol	Strasser (1992)
	20.40	16.80	1.21				Harvey et al. (1987)
<i>Pongo pygmaeus</i>	86.30 (4)	38.70 (5)	2.23	3	A	Frug	Markham and Groves (1990) (Borneo)
	86.20 (1)	38.30 (5)	2.25				Markham and Groves (1990) (Sumatra)
<i>Presbytis comata</i>	72.58 (8)	36.41 (11)	1.99	3	A	Fol	Hrdlicka (1925)
	85.62 (4)	38.78 (4)	2.21				Lyon (1908a)
	81.70 (10)	37.80 (10)	2.16				Jungers (1985) <i>P. p. pygmaeus</i>
	77.50 (3)	37.7 (6)	2.06				Jungers (1985) <i>P. p. abelli</i>
	83.60	37.80	2.21				Rodman (1984)
	69.00	37.00	1.86				Harvey et al. (1987)
	6.68 (3)	6.66 (4)	1.00				Strasser (1992)
	6.30	6.20	1.02				Harvey et al. (1987)
	6.60 (13)	5.70 (25)	1.16				Oates et al. (1995)
	6.75 (7)	5.79 (12)	1.16				Schultz (1940)
<i>Presbytis cristatus</i> ¹⁶	6.93 (6)	5.95 (6)	1.16	3	A/T	Fol	Jungers (1985)
	6.58 (1)	6.12 (1)	1.08				Lyon (1908b)
	6.42 (7)	5.50 (4)	1.17				Strasser (1992)
	8.60	8.10	1.06				Harvey et al. (1987)
	10.64 (7)	6.70 (3)	1.59				Napier (1985) (<i>P. e. theristes</i>)
	20.00 (2)	15.30 (3)	1.31				Napier (1985) (<i>P. e. schistacea</i> group)
	13.04 (9)	9.89 (11)	1.32				Napier (1985) (<i>P. e. entellus</i> , <i>hypoleucos</i> , and <i>priam</i> groups)
	12.75 (19)	9.42 (20)	1.35				Napier (1985) (all specimens in the BMNH)
	19.80 (3)	15.60 (5)	1.27				Oates et al. (1995) (<i>P. e. "schistacea"</i>)
	18.30 (3)	11.20 (22)	1.63				Blaffer Hrdy (1977) cited in Oates et al. (1995) (<i>P. e. entellus</i>)
<i>Presbytis entellus</i> ¹⁷	18.40	11.40	1.61	4	A/T	Fol	Harvey et al. (1987)
	15.20	10.40	1.46				Gaulin and Sailer (1984)
	12.70 (4)	10.90 (1)	1.16				Oates et al. (1995)
	14.80	12.00	1.23				Harvey et al. (1987)
<i>Presbytis johnii</i>	18.40	11.40	1.61	3	A	Fol	Harvey et al. (1987)

APPENDIX A. (continued)

Species	Male weight	Female weight	Dim	Com	Sub ¹	Diet ²	Reference
<i>Presbytis melalophos</i>	6.48 (25)	6.32 (27)	1.02	3	A	Fol	Strasser (1992)
	6.52 (6)	6.92 (1)	0.94				Lyon (1908b)
	7.03 (1)	6.46 (1)	1.09				Napier (1985)
	6.68 (2)	6.88 (3)	0.97				Fleagle (1976)
	5.90	5.80	1.02				Oates et al. (1995)
	7.00	6.60	1.06				Roonwal and Mohnot (1977)
	6.70	6.60	1.02				Harvey et al. (1987)
	6.20	6.00	1.03				Gaulin and Sailer (1984)
	7.39 (15)	6.47 (36)	1.14				Burtin (1981)
	7.32 (12)	6.60 (22)	1.11				Napier (1985)
<i>Presbytis obscurus</i> ¹⁸	7.54 (7)	6.08 (8)	1.24	3	A	Fol	Jungers (1985)
	7.90 (3)	5.98 (3)	1.32				Fooden (1976) (Ban Thap Plik)
	7.95 (2)	5.50 (5)	1.44				Fooden (1976) (Ban Kuan Daeng)
	7.20 (6)	6.90 (2)	1.04				Fooden (1976) (Ban Palian)
	7.94 (4)	7.35 (5)	1.08				Strasser (1992)
	7.58 (2)	6.60 (2)	1.15				Fleagle (1976)
	8.30	6.50	1.28				Harvey et al. (1987)
	6.30	6.00	1.05				Gaulin and Sailer (1984)
	5.77 (4)	5.14 (2)	1.12				Napier (1985)
	12.80 (2)	10.00 (3)	1.24				Oboussier and von Maydell (1959) cited in Oates et al. (1995)
<i>Presbytis pileatus</i> ¹⁹	12.80	10.10	1.27	3	A	Fol	Green (1981)
	12.75	10.40	1.22				Gaulin and Sailer (1984)
	6.50 (6)	6.40 (4)	1.02				Tilson and Tenaza (1976)
	6.20 (18)	5.70 (21)	1.09				Oates et al. (1995)
	6.24 (18)	6.38 (9)	0.98				Strasser (1992)
	6.19 (6)	5.68 (6)	1.09				Jungers (1985)
	6.27 (5)	5.60 (6)	1.12				Schultz (1940)
	6.74 (9)	6.50 (7)	1.04				Lyon (1908a)
	6.30	6.30	1.00				Harvey et al. (1987)
	5.67 (1)	5.11 (2)	1.11				Napier (1985) (<i>P. v. vetulus</i>)
<i>Presbytis vetulus</i> ²¹	9.42 (2)	7.49 (1)	1.26	3	A/T	Fol	Napier (1985) (<i>P. v. monticola</i>)
	8.17 (3)	5.90 (3)	1.38				Napier (1985) (combined sample)
	8.50	7.80	1.09				Harvey et al. (1987)
	19.00 (5)	11.70 (8)	1.62				Dechow (1983)
	20.12 (2)	11.45 (4)	1.76				Field notes, MNHN
	20.50	13.60	1.51				Harvey et al. (1987)
	7.18 (19)	5.18 (16)	1.39				Ayres (1986) cited in Ford and Davis (1992)
	7.38 (8)	5.47 (10)	1.35				Rosenberger and Strier (1989)
	8.28 (4)	5.41 (3)	1.53				Jungers (1985)
	6.53 (3)	4.93 (3)	1.32				Rosenberger and Strier (1989)
<i>Alouatta caraya</i>	6.22 (3)	4.53 (3)	1.37	4	A	Fol	Rosenberger and Strier (1989)
	7.16 (10)	5.60 (10)	1.28				Rosenberger and Strier (1989)
	8.40 (1)	6.35 (2)	1.32				Milton (1984) cited in Ford and Davis (1992)
	7.40 (1)	6.35 (1)	1.16				Schultz (1940)
	7.67 (2)	5.92 (2)	1.30				Schultz (1941)
	7.94 (2)	6.58 (2)	1.21				Crile and Quiring (1940)
	7.90	6.30	1.25				Milton (1982) cited in Ford and Davis (1992)
	11.59 (1)	6.29 (3)	1.84				Jungers (1985)
	11.11 (1)	6.58 (1)	1.69				Murie (1935) cited in Ford and Davis (1992)
<i>Theropithecus gelada</i>				4	S	Frug	
<i>Alouatta belzebul</i>				4	A	Fol	
<i>Alouatta caraya</i>				4	A	Fol	
<i>Alouatta fusca</i>				4	A	Fol	
<i>Alouatta palliata</i>				4	A	Fol	
<i>Alouatta pigra</i>				4	A	Fol	

APPENDIX A. (continued)

Species	Male weight	Female weight	Dim	Com	Sub ¹	Diet ²	Reference
<i>Alouatta seniculus</i>	7.62 (28)	6.02 (34)	1.26	4	A	Fol	Ayres (1986) cited in Ford and Davis (1992)
	9.00 (1)	5.20 (1)	1.73				Mittermeier (1977) cited in Ford and Davis (1992)
	7.88 (3)	5.50 (5)	1.43				Jungers (1985)
	6.92 (10)	5.30 (10)	1.31				Rosenberger and Strier (1989)
	6.69 (2)	5.50 (1)	1.22				Peres (1993)
<i>Aotus lemurinus</i> ²²	8.06 (1)	6.35 (1)	1.27	1	A	Frug	Fooden (1964)
	7.00 (1)	6.5 (1)	1.08				Husson (1978)
	0.89 (6)	0.92 (11)	0.97				Crile and Quiring (1940)
	0.92 (1)	0.93 (1)	0.99				Ayres (1986) cited in Ford and Davis (1992)
	8.38 (2)	6.70 (8)	1.25				Fedigan et al. (1988)
<i>Ateles geoffroyi</i>	7.42 (22)	8.00 (34)	0.93	2	A	Frug	Schultz (1940)
	7.45 (20)	7.64 (32)	0.98				Schultz (1941)
	7.79 (6)	8.91 (14)	0.87				Crile and Quiring (1940)
	9.45 (16)	8.59 (35)	1.10				Ayres (1986) cited in Ford and Davis (1992)
	8.16 (1)	7.03 (1)	1.16				Murie (1935) cited in Ford and Davis (1992)
<i>Ateles paniscus</i>	7.86 (4)	7.69 (7)	1.02	2	A	Frug	Mittermeier (1977) cited in van Roosmalen (1985)
	9.61 (4)	8.38 (4)	1.15				Lemos de Sa and Glander (1993)
	14.40 (2)	12.00 (1)	1.20				Rushi (1964) cited in Ford and Davis (1992)
	3.45 (1)	2.88 (2)	1.20				Ayres (1986) cited in Ford and Davis (1992)
	0.84 (1)	0.85 (1)	0.99				Hershkovitz (1990)
<i>Callicebus brunneus</i>	1.08 (5)	0.99 (12)	1.09	1	A	Frug	Ayres (1986) cited in Ford and Davis (1992)
	1.02 (3)	0.88 (6)	1.16				Hershkovitz (1990)
	1.27 (5)	1.38 (6)	0.92				Hershkovitz (1990)
	1.10 (1)	1.31 (6)	0.84				Hershkovitz (1990)
	0.21	0.24	0.87				Coimbre-Filho and Mittermeier (1978) cited in Ford and Davis (1992)
<i>Callicebus personatus</i>	0.11 (36)	0.12 (27)	0.92	1	A	Fr/Ins	Soini (1988) cited in Ford and Davis (1992)
	0.12 (1)	0.11 (1)	1.09				Peres (1993)
	0.11	0.12	0.92				Robinson and Ramirez (1982) cited in Ford and Davis (1992)
	0.15	0.14	1.07				Coimbra-Filho and Mittermeier (1978) cited in Ford and Davis (1992)
	0.16	0.14	1.14				Ayres (1986) cited in Ford and Davis (1992)
<i>Callicebus moloch</i>	3.37 (20)	2.45 (21)	1.38	4	A	Fr/Ins	Ayres (1986) cited in Ford and Davis (1992)
	3.30 (20)	2.50 (22)	1.32				Lucas et al. (1986) cited in Ford and Davis (1992)
	3.33 (8)	1.94 (8)	1.72				Jungers (1985)
	4.50 (1)	3.10 (1)	1.45				Husson (1978)
	3.22 (2)	1.77 (1)	1.82				Hill (1960) cited in Ford and Davis (1992)
<i>Cebus apella</i>	2.93 (16)	2.18 (20)	1.34	3	A	Fr/Ins	Field notes, USNM
	2.23 (2)	1.59 (1)	1.40				Hill (1960) cited in Ford and Davis (1992)
	4.50 (1)	3.20 (1)	1.41				Mittermeier (1977) cited in Ford and Davis (1992)
	2.88 (18)	2.66 (21)	1.08				Ayres (1986) cited in Ford and Davis (1992)
	2.90 (20)	2.58 (19)	1.12				Hershkovitz (1985)
<i>Chiropotes satanas</i> ²³	3.50 (1)	2.50 (1)	1.40	2	A	Frug	Husson (1978)

APPENDIX A. (continued)

Species	Male weight	Female weight	Dim	Com	Sub ¹	Diet ²	Reference
<i>Lagothrix lagothricha</i> ²⁴	6.67 (6)	5.54 (7)	1.20	2	A	Fr/Ins	Ayres (1986) cited in Ford and Davis (1992) Fooden (1963) (<i>L. l. lagothricha</i>) Fooden (1963) (<i>L. l. poeppigii</i>) Peres (1993) (<i>L. l. cana</i>) Jungers (1985)
	8.10 (4)	5.74 (5)	1.41				
	4.30 (2)	6.00 (1)	0.73				
	10.20 (1)	7.65 (1)	1.33				
<i>Leontopithecus rosalia</i> ²⁵	8.77 (8)	5.74 (4)	1.53	2	A	Fr/Ins	Rosenberger and Coimbra-Filho (1984)
	0.51 (9)	0.48 (11)	1.06				
<i>Pithecia pithecia</i> ²⁶	1.80 (4)	1.51 (4)	1.19	2	A	Frug	Ayres (1986) cited in Ford and Davis (1992) Fooden (1964) Husson (1978) Oliveira et al. (1985)
	1.84 (2)	1.53 (1)	1.20				
	1.92 (2)	1.51 (3)	1.27				
	1.97 (6)	1.59 (3)	1.24				
<i>Saimiri boliviensis</i> <i>Saimiri oerstedj</i> ²⁷	1.10 (1)	0.70 (1)	1.57	3	A	Fr/Ins	Ford and Davis (1992) Boinski (1989) Schultz (1940) Schultz (1941)
	0.75	0.60	1.25				
	0.89 (8)	0.74 (4)	1.20				
	0.89 (8)	0.79 (4)	1.13				
<i>Saimiri sciureus</i>	0.96 (11)	0.79 (9)	1.22	3	A	Fr/Ins	Jungers (1985) Sanderson (1949) cited in Ford and Davis (1992) Ayres (1986) cited in Ford and Davis (1992) Peres (1993)
	1.05 (2)	0.78 (8)	1.35				
	0.91 (4)	0.81 (6)	1.12				
	0.95 (1)	0.54 (1)	1.76				
<i>Saguinus fuscicollis</i>	0.74 (7)	0.58 (5)	1.28	2	A	Fr/Ins	Fooden (1964) Garber and Teaford (1986) Ayres (1986) cited in Ford and Davis (1992) Yoneda (1981) cited in Ford and Davis (1992) Peres (1993) (<i>S. f. melano-leucus</i>) Peres (1993) (<i>S. f. fuscicollis</i>)
	0.41 (33)	0.41 (11)	1.00				
	0.42 (4)	0.37 (4)	1.14				
	0.40 (4)	0.42 (3)	0.95				
	0.44 (1)	0.40 (1)	1.10				
	0.41 (1)	0.41 (4)	1.00				
<i>Saguinus labiatus</i>	0.48 (34)	0.52 (18)	0.92	2	A	Fr/Ins	Snowdon and Soini (1988) cited in Ford and Davis (1992) Yoneda (1981) cited in Ford and Davis (1992) Buchanon-Smith (1991) Ayres (1986) cited in Ford and Davis (1992)
	0.49 (17)	0.50 (12)	0.98				
	0.46 (6)	0.46 (3)	1.00				
	0.49 (4)	0.52 (1)	0.94				
<i>Saguinus midas</i> ²⁸	0.58 (2)	0.60 (1)	0.97	2	A	Fr/Ins	Husson (1978) Hill (1957) cited in Ford and Davis (1992) Hill (1957) cited in Ford and Davis (1992) Sanderson (1949) cited in Ford and Davis (1992)
	0.33 (1)	0.33 (2)	1.00				
	0.26 (1)	0.31 (2)	0.84				
	0.60 (5)	0.53 (5)	1.13				
<i>Saguinus mystax</i> ²⁹	0.57 (18)	0.58 (10)	0.98	2	A	Fr/Ins	Garber et al. (1993) Robinson and Ramirez (1982) Garber and Teaford (1986) Peres (1993) (<i>S. m. mystax</i>)
	0.50 (2)	0.53 (2)	0.94				
	0.56 (16)	0.62 (11)	0.90				
	0.50 (1)	0.55 (2)	0.91				
<i>Saguinus oedipus</i>	0.48 (55)	0.50 (40)	0.96	2	A	Fr/Ins	Dawson and Dukelow (1976) Neyman (1978)
	0.40 (6)	0.43 (12)	0.93				

¹ A = arboreal; A/T = arboreal/terrestrial; S = savanna.² Fol = folivorous; Frug = frugivorous; Fr/Ins = frugivorous/insectivorous.³ This species shows large geographic variation in body weight and dimorphism estimates. Napier's (1981) data are used for this analysis because they yield a value of dimorphism near the mean value of dimorphism among all sources cited here. Jungers (1985) data are abstracted from Rothenfluh (1976).⁴ Oates et al. (1995) report values cited from both Napier (1985) and W.L. Jungers (personal communication). The competition level has been changed from level 3 (Plavcan and van Schaik, 1992) to level 4 following the report of von Hippel (1996).⁵ Napier's (1985) data are used for this analysis. Struhsaker's (1975) data appear to be commonly cited in the literature (e.g., Harvey et al., 1987). Gaulin and Sailer (1984) do not specify the source of their data for this species. Oates et al.'s (1995) data yield unusually low dimorphism by comparison to the other estimates.⁶ Oates et al. (1995) report values that include data cited as a personal communication from W.L. Jungers.⁷ Weights are for the "Angka" series of specimens reported by Schultz (1944).

APPENDIX A. (continued)

⁸ Jungers (1985) also cites the Museum of Comparative Zoology as a source for his data, so that the values reported here probably include at least some specimens reported by Jungers (1985).

⁹ Napier (1981) reports body weight values for all specimens in the British Museum, without regard to subspecies. The values used in this analysis are only for specimens of *M. mulatta mulatta*.

¹⁰ Estimates of weight dimorphism in this species are highly divergent, with Harvey et al.'s (1987) estimates yielding unusually low dimorphism by comparison to other estimates. Apparently, *M. n. pagensis* is substantially smaller than other subspecies (Miller, 1903), suggesting that perhaps variation in body weight and weight dimorphism estimates is a consequence of mixing data from different subspecies. Fooden (1976) reports a single female weight of 5.45 kg, and a "late subadult" male weight of 9.75 kg, yielding dimorphism of 1.79.

¹¹ Weights reported by Lyon (1908a,b) are from specimens collected by W.L. Abbot on Borneo and adjacent islands (1908a) and in western Borneo (1908b). Weights reported by Oates et al. (1995) are cited as a personal communication from W.L. Jungers.

¹² Jungers' (1985) values are used because the sample size is the largest, and the value of dimorphism is intermediate to those of other reports.

¹³ Jungers and Sussman's (1984) values are used because the sample size is the largest, and the value of dimorphism is intermediate to those of other reports. However, weights from that study include weights reported on the same subspecies by Rahm (1967) and Wrangham and Smuts (1980). Weights from Wrangham and Smuts (1980) and Uehara and Nishida (1987) include data taken on the same individuals over a period of time.

¹⁴ Values reported by Strum (1991) are for a population that regularly raids crops, and one that does not. The taxonomic classification of baboon species is irregular. Baboons (including *Papio cynocephalus*, *P. anubis*, *P. ursinus*, and *P. hamadryas* are variously recognized as a single species, two species, or even five species (Jolly, 1993). Dechow (1983) demonstrates significant differences in body size among the various groups. For this reason, we include the groups separately in the analysis. Our listing of the groups as separate species is primarily for convenience, and is not an endorsement of a particularly taxonomic hypothesis.

¹⁵ Napier (1981) reports values separately for *P. cynocephalus*, and for *P. c. kindae*, which is substantially smaller than other baboons (and is recognized as a separate species by some; we follow Napier's classification in this case for consistency with the source of body weight data). The values of *P. c. kindae* are used in this analysis specifically because dental samples used to investigate canine dimorphism (Plavcan, 1990, 1993; Plavcan and van Schaik, 1992; Plavcan et al. 1995) utilize the Kinda baboon, and the values of dimorphism for the two samples are quite close.

¹⁶ Oates et al. (1995) report weights cited as a personal communication from W.L. Jungers.

¹⁷ This species shows substantial intraspecific variability in body size. Napier (1985) reports values for all specimens in the British Museum, and for specific groups of subspecies. The values used here are for *P. e. thersites* because this is the only set of figures reported by Napier specifically for a single subspecies, and because this subspecies was used by Plavcan (1990, 1993). Plavcan and van Schaik (1992), and Plavcan et al. (1995) for studies of canine dimorphism. Oates et al. (1995) report body weight data for *P. e. schistacea* from Blaffer Hrdy (1977), Bishop (unpublished data), and Napier (1985). Napier (1985) reports weights for the *P. e. schistacea* group, which includes *P. e. ajax*. It is not clear if Napier (1985) actually includes weights for both subspecies.

¹⁸ Some of Burtin's (1981) specimens are stored in the British Museum (Natural History). Therefore, Napier's (1985) values probably include part of Burtin's sample. Fooden reports specimens by collection locality. Note that values of dimorphism for Fooden's specimens are substantially greater than those for Burtin's and Napier's values. Burtin's (1981) sample was used because of the large sample size collected from a restricted geographic area.

¹⁹ Green (1981) cites values for museum specimens cited in Oboussier and von Maydell (1959) and Pocock (1939).

²⁰ Oates et al. (1995) report weights cited as a personal communication from W.L. Jungers.

²¹ Napier (1985) cites body weights for two subspecies. However, dimorphism calculated for weights from the individual subspecies differs. The value for *P. v. vetulus* is used in this analysis (in spite of the small sample size) because it yields dimorphism that is intermediate between that for *P. v. monticola* reported by Napier (1985), and the figures reported by Harvey et al. (1987).

²² Crile and Quiring (1940) actually cite weights of 8.89 kg and 9.16 kg—clearly a typo—for "*Aotus zonalis*" of Panama.

²³ Data from Herschkovitz (1985) are for *C. satanas chiroptotes* abstracted from Ayres (1981), and specimens from the Field Museum of Natural History, National Museum of Natural History, and Museu Paraense Emílio Goeldi, Belem. The competition level has been changed from level 1 (Plavcan and van Schaik, 1992) to level 2 following Ford (1994).

²⁴ Peres (1993) reports additional male body weights of 8.93 and 9.35 kg. However, these are for specimens that were eviscerated, and the full weight was calculated by extrapolating the weight of the internal organs from an allometric regression.

²⁵ Rosenberger and Coimbra-Filho (1984) also provide the following data for other species of *Leontopithecus*: *L. chrysomelas*, male weight = 0.62 (n = 2), female weight = 0.53 (n = 6); *L. chrysopagus*, male weight = 0.58 (n = 4). The competition level has been changed from level 1 Plavcan and van Schaik (1992) to level 2 following the classification of males by Plavcan et al. (1995) as high-frequency, low-intensity male-male competition.

²⁶ Husson (1978) cites Sanderson (1949) for the female body weights.

²⁷ Boinski (1989) specifies that male weights are taken outside of the breeding season. This suggests that the estimate of dimorphism is low compared to that present during the breeding season, since males are reported to increase in body weight substantially during the breeding season. Since Schultz does not specify when male weights were gathered, Boinski's data are preferred for this analysis, even though sample sizes are not reported.

²⁸ As pointed out by one reviewer of this paper, the values reported by Sanderson (1949) contain an extreme outlier. Excluding this specimen, the male mean is reduced to 0.491 kg, yielding dimorphism of 0.93. For this reason, Ayres (1986) data are preferred. The competition level of all *Saguinus* species has been changed from level 1 (Plavcan and van Schaik, 1992) to level 2 following the classification of males by Plavcan et al. (1995) as high-frequency, low-intensity male-male competition.

²⁹ Values reported from Garber et al. (1993) are for the oldest of three adult age classes. The youngest class yields data of (M = 0.55, n = 6, F = 0.56, n = 13) for dimorphism of 0.98, and the intermediate age class yields values of (M = 0.54, n = 6, F = 0.56, n = 6) for dimorphism of 0.96. The value of the male reported by Peres (1993) is listed as "500+" grams.